

Putting Heads in Bags

THE continuing civil disturbance in Northern Ireland is an important counterpoise against the reputation of the United Kingdom for orderly political processes, but most outsiders have in the past few years been willing to acknowledge that the tension between the Protestant and Catholic communities, exacerbated as it is by poverty, is an intractable social problem. This, at least, was the case until the beginning of August this year, when arrangements were made to detain some hundreds of people under emergency regulations which gave those detained no right of access to the courts. It is fair to say that the governments of Northern Ireland and of the United Kingdom have been reluctant to resort to these measures and even their most severe critics will agree that the decision in favour of internment, right or wrong, was a response to growing violence. In retrospect, of course, it may have been a gross miscalculation to have supposed that detention without trial would have solved important problems. The most serious damage to the reputations of the two governments concerned will, however, in the long run be seen to depend not so much on the process of detention as on the gloss which the government of the United Kingdom has managed to put on some of the events accompanying detention as a result of a report by a committee under Sir Edmund Compton "into allegations against the security forces of physical brutality in Northern Ireland arising out of events on the 9th August, 1971" (Cmnd 4823, HMSO, £0.525).

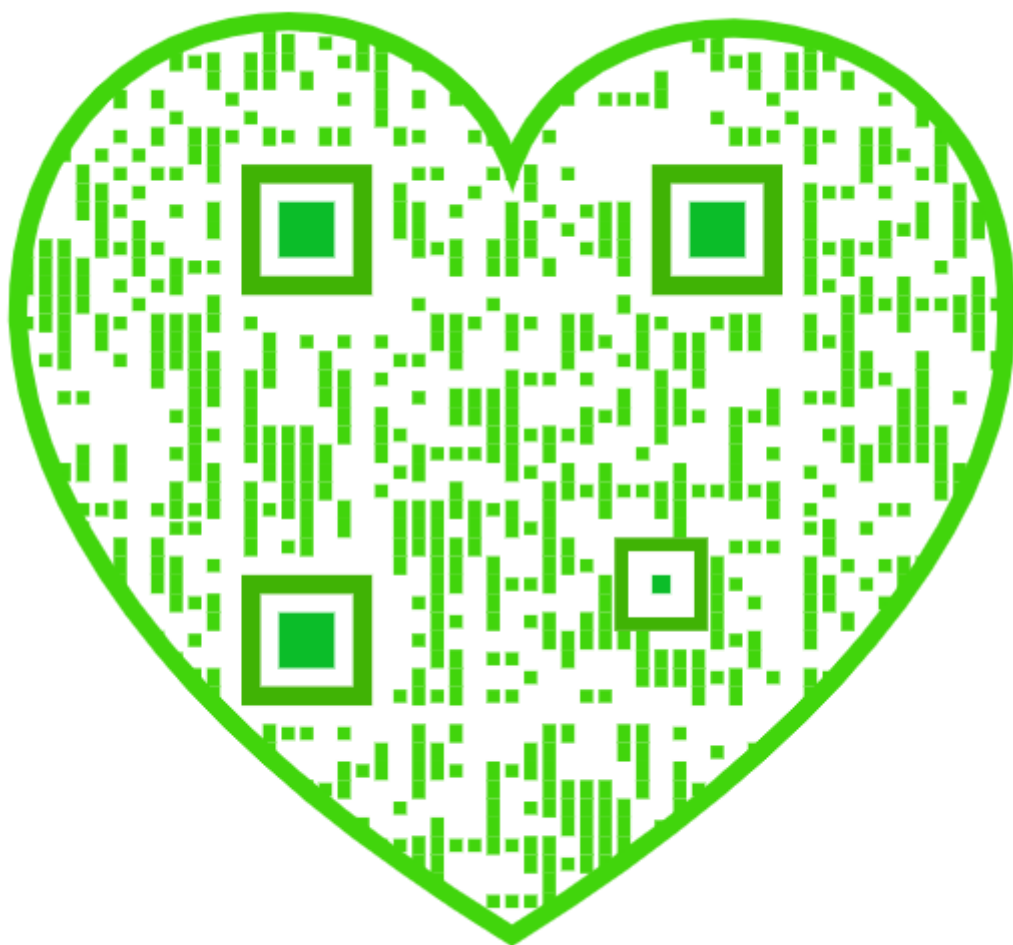
The circumstances which provoked the report, chiefly allegations by prisoners and their relatives of brutal treatment by their captors, are less shocking than the report of the Compton inquiry, which affects a conveniently pedantic definition of brutality and a disturbing ignorance of the damage that may be done to people by some of the devices which its own proceedings established to have been used in Northern Ireland. Many of the allegations against the British army and the police forces of Northern Ireland are familiar from recent accounts of the ill-treatment of prisoners in places such as Greece and North Korea. Broadly speaking, the Compton inquiry has confirmed the statements of newspapers such as the *Sunday Times* earlier this year that prisoners had been subjected to indignities such as having their heads covered with opaque bags except during interrogation and in solitude, being required to stand facing a wall with legs apart for periods of several hours at a time, being subjected to electronic noise while in a crowd together and being fed with bread and water. The report of the Compton inquiry says that "it was the general policy to deprive the men of opportunity to sleep during the early days of the operation".

Other allegations against the army include tales of being forced into helicopter journeys, according to the army so as to persuade on-lookers that prisoners were being moved elsewhere and according to the prisoners as an attempt to frighten them, and the Compton inquiry says in its report that "it is understandable that they

should have been frightened by the unknown and should have thought in the absence of any other reasons that the intention must be to victimize them by putting them through a meaningless exercise involving physical hurt or the threat of it. . . . They seem to have suffered no physical damage but we think the physical experience they were forced to go through under these circumstances does constitute a measure of ill-treatment." Elsewhere, at a military prison at Ballykinler Camp, prisoners were required to perform painful physical exercises for long periods of time and the Compton inquiry says "We think it is plain that these compulsory exercises must have caused hardship to some at least of those who were made to do them, especially those in poor physical condition. . . . On the other hand we do not regard the exercises as cruel, if the adjective means that the exercises were thought of and carried out with a view to hurting or degrading the men who had to do them. We prefer to take the view that the exercises were devised to counteract the cold and the stiffness of which the arrested persons complained, but that it should have been foreseen that a system of voluntary changes of position at set times was bound to turn into a form of physical drill compulsorily performed without regard to the relative capacity of the performers, and that the routine was thoughtlessly prolonged after it had served its proper purpose. We think there was lack of judgment here, but not cruelty or brutality, and we think the complainants may have suffered hardship but we made no findings of deliberate ill-treatment."

To its credit, the commission does publish in its report detailed accounts of how individual prisoners were treated and ill-treated. The commission says that it was probably wrong to have discharged Mr Elisha Anderson, at fifty-five and with a chronic heart condition, barefoot into a road strewn with rubble, that Mr Gerard Campbell, whose wrists had been tied and head covered with a sandbag, was so dealt with because of an order which "showed lack of judgment", that Mr William Gilmore was injured by a rubber bullet fired without cause, that Mr Joseph Hughes was held in what is called the "Kado" grip, the effect of which "can be harsh, but it is a recognized method for the controlled use of force", and that Mr J. Moore was roughly and wrongly arrested. In short, the inquiry provides a wealth of evidence to show that the army dealt roughly with its prisoners on August 9 this year. The question is whether the army was brutal.

The Compton inquiry's argument on this point is indefensible. The committee says that having been asked to deal with allegations of physical brutality, "we have confined our investigation to that part of the complaint that relates to physical treatment". The committee goes on to say that brutality is an "inhuman or savage form of cruelty and that cruelty implies a disposition to inflict suffering coupled with indifference to or pleasure in the victim's pain". In all the particular cases listed in the report of the inquiry, it is held that these criteria are not satisfied. Instead, the argument goes, the way in which



the prisoners were dealt with constituted not "brutality" but "ill-treatment". In passing, of course, it will be remarked that this is largely a semantic point. In dealing with allegations against an army or a police force, it is plainly unreasonable to ask whether the person carrying out orders to deal roughly with a prisoner has a "disposition to inflict suffering" and it is entirely conceivable that he may execute these orders with such reluctance that he is neither indifferent to his victim's condition nor moved to pleasure by it. In short, the definition of brutality which the Compton inquiry chose to use is one almost certain to ensure that it could not be applicable to the allegations which had been made in Ulster. If this was its starting point, the commission might have saved itself and its witnesses the trouble of having gone to Belfast.

The more serious point of pedantry, however, is the commission's sharp distinction between physical ill-treatment, brutal or otherwise, and other forms of ill-treatment, presumably psychological. It is not necessary to invoke Freud to know that the distinction is unreasonable and untenable. The experience of recent wars has shown plainly enough that assault on a person's sensory apparatus can cause profound physical disturbance. By now, there is also a substantial amount of carefully controlled psychological experiment to show how harmful may be the effects, psychological and otherwise, of sensory deprivation. Professor Patrick Wall and some of his associates have in the past few days been pointing to

the evidence accumulated in the past fifteen years which shows how anxiety can be induced by hooding in a few hours, and how enforced sleeplessness can induce psychotic behaviour. It goes without saying that in circumstances like these, prisoners are highly suggestible and therefore likely to be unreliable witnesses. Would the Compton commission have been as sanguine in its statement of the irrelevance of the psychological consequences of the treatment to which prisoners have been subjected in Ulster if it had known of the similarity between the effects of enforced hooding and the effects of treatment with mescaline and other types of hallucinogenic drug?

It is too soon to know what will be the outcome of this shabby inquiry. The wider investigation now begun under Lord Parker may help to provide a better perspective. The most serious danger in the Compton report is not the immediate risk that it may sanction methods of ill-treatment which are disgusting, but that it will somehow help to sanctify the false belief that it is permissible and even possible to distinguish between physical and psychological brutality. To a nation such as Britain, with a long record of denying the unconscious, this may be a palatable conclusion. It is, however, wrong and it is potentially dangerous not merely for the permanent harm which psychological ill-treatment can do to prisoners but for the damage which may be done to society at large by the casual acceptance of psychological brutality in the maintenance of law and order.

The Faster than Sound Machine

IN the marriage of national pride with which the British and French governments have invested £850 million in the development of the Concorde aircraft, it has usually seemed as if all the ardour was French and that the British government would have been glad of any excuse to break its contract. Mr Roy Jenkins, who became Minister of Aviation in the Labour government in 1964, made no secret of his annoyance that those who had negotiated the agreement to develop the aircraft had deliberately omitted provisions to regulate the way in which one party might bow out. Over the years, British governments have first shuddered at the rising cost of development, now four times the first estimate, and have then decided to whistle so as to keep their spirits up by saying that it would be folly to back out of a development project which had already cost a very large sum of money and which, in any case, would give Britain and France in partnership a sense or an illusion of "technological leadership".

This is the spirit in which the British government last week dropped all its reluctance about the Concorde project. First of all, on December 7, the two governments agreed in Paris on what is called a pricing formula to be used in negotiations between the manufacturers and potential purchasers of the aircraft. The formula is a device for saying that the two governments will not seek to recover a contribution towards the money spent on development, at least where the first sales are concerned. At the same time, the two governments let it be known that they would encourage the British Overseas Aircraft Corporation and Air France to place firm orders for

Concorde aircraft—an open invitation to the airlines concerned to ask for a subsidy. Indeed, there is even talk of the possibility that airlines purchasing Concorde aircraft may be helped along with operating costs as well as with capital. Yet it remains a simple truth that the airlines are not falling over themselves to order this remarkable aircraft. This is why it is still proper to ask awkward questions about the whole project and to ask whether, even at this late stage, it may yet be wisest to abandon the Concorde.

Technically, of course, there is no cause for complaint. Everybody says that the aircraft performs well and, even if the excited applause of ministers fresh from their first flight is no substitute for hard-headed technical appraisal, it seems now to have been demonstrated that the construction of supersonic passenger transport aircraft is technically feasible. Moreover, Concorde is less of an environmental nuisance than has sometimes been supposed. The engines are noisier than they might be, it is true, but nobody is seriously worried about the effects of exhaust gases on the stratosphere and sonic booms can be diminished by keeping the aircraft over the sea for the faster part of its trajectory. In other words, the Concorde has helped to demonstrate that it can only be a matter of time before supersonic aircraft are in regular airline service, providing passengers with the immense convenience of faster long-distance journeys and providing airlines with profits commensurate with the service they will then be able to provide.

The doubts about the Concorde centre not on the rights and wrongs of supersonic flights as such but on the

economics of this particular machine. Will it do the job it is intended to perform at anything like the cost that would make the operation profitable? And will airlines be able at this stage in their history to afford the expensive re-equipment which the arrival of the Concorde would imply? The new machine must necessarily be a great economic hazard for those who buy it. However the initial cost of the aircraft may be reduced by what the governments of Britain and France are pleased to call their "pricing formula", the operating costs will be unpleasantly high simply because the aircraft carries so few passengers—a mere 165 or so. Precisely what the total cost will be is likely to be apparent only when airlines have had experience of how quickly these machines can be turned round at each end of a journey. At least if the Concorde is intended to be operated as a commercial proposition, everything will depend on keeping equipment in the air as continuously as possible, and the discussion which preceded the abandonment of the American SST earlier this year showed that airlines are as bemused as anybody by the difficulties of calculating in advance precisely how these aircraft would be operated.

What this implies is that the decision to bring the Concorde into airline service is a leap into the dark for any operator. Prudent people would assume that the possession of a fleet of supersonic aircraft will mean losses. In other words, there is a serious danger that the only customers for the aircraft will be those whose governments persuade them that it is their patriotic duty to place an order. Although Pan-American World Airways is the best potential outlet for sales among strictly commercial airlines, its recent bout of heart-searching may have given it a greater sense of realism than when it first took out an option. Only time will tell. But if it should turn out that the only potential customers for the Concorde are the two national nationalized airlines, then the best course which the sponsoring governments can pursue will be to swallow their pride and cancel the aircraft. In doing so, they will have to acknowledge, painful though that acknowledgment may be, that there is a world of difference between a successful demonstration of the potential benefits of supersonic flight and the development of a commercially successful method for realizing that goal.

Television Frequencies for Grabs

THE 1970s will be formative years for the pattern of broadcasting in Britain, and already there are several signs of the way the wind is blowing. Since the summer, the British government, true to its election promises, has been waving on the bidders for licences to operate commercial radio broadcasting stations. Although such enterprises may not be as profitable in Britain as they are in the United States, long before the end of the decade, the British Broadcasting Corporation will be but one of the sources of broadcast sound. By 1976, however, the government will also have had to make up its mind about the revision and extension of the BBC's charter. The crucial question is the arrangement to be made for television broadcasting, which is why the government should not respond too quickly to the claim last week by the Independent Television Authority for a second television channel for the commercial companies which at present broadcast commercial television signals. The ITA's case is stronger than out-and-out critics of commercial broadcasting will allow, but it would be wrong to make lasting commitments to commercial companies while the future pattern of television broadcasting is undefined.

Within the present framework of broadcasting in Britain, the ITA has a strong case for a second television channel. In its statement last week, the authority said that it is anxious to provide a better service by providing a wider range of programmes. The argument is that while there is only one commercial television channel, the companies have no option but to try to attract the largest possible audience. Although the commercial network in Britain has done some distinguished broadcasting in its time (since the mid-1950s), most of its programmes are undistinguished. What the Independent Television Authority is now asking, on behalf of the programme companies, is that there should be a second channel so that the companies will be able to compete not merely for the mass audience but for what is sometimes called

the minority audience and which is at present the theoretical preserve of BBC-2.

The ITA is right to claim that diversification will come about naturally only if the second channel is made available to the companies already blessed with a franchise to operate the first. Throwing the second channel open to a new group of operating companies would merely create a situation in which two parallel commercial networks were competing for the same mass audience, presumably with programmes devised so as to rival each other in imbecility. The difficulty is that if the programme contractors recognize that a second channel endowed with a smaller audience will be a poor magnet for advertising revenue, its programmes will be impoverished by parsimony. (Too much success might create other difficulties, and might, for example, further undermine the British newspaper industry by siphoning off advertising revenue.) The extent to which the ITA would be able to make the programme contractors toe a more enlightened line is another imponderable—in the past, contracting companies have been able to wriggle off painful hooks by pleading poverty.

The most serious argument against the new proposals is not, however, that they may not work as the ITA now promises but that it is quite absurd that a country such as Britain should at this point commit itself to a pattern of television broadcasting which provides for merely four channels. Why is so little use being made of the 376 MHz of the UHF band given over to television broadcasting in Britain? This substantial slice of the spectrum has been divided into channels each 8 MHz wide, and care has been taken to construct a network of broadcasting masts which provides respectable coverage of most parts of Britain (with the notorious exception of northern Scotland). The intention has been to build a network which can provide the whole country with the same service. What this implies is that if one transmitter is given four channels on which to broadcast two UHF signals for

the BBC and two for the commercial television companies, each neighbouring transmitter must be given four entirely different channels so as to avoid radio interference. The result, of course, is that the available bandwidth is rapidly consumed.

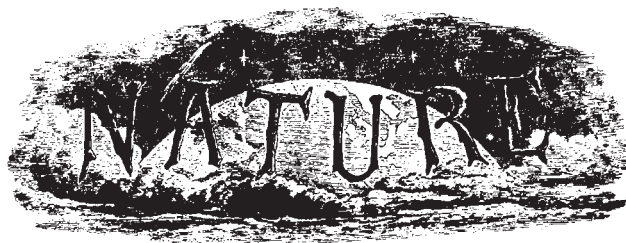
If there is to be a uniform television service for the whole of Britain, there is no doubt that the available band-width is sufficient for only four separate networks of programmes. The question that should be asked, however, is whether it is necessary, let alone desirable, to provide a strictly uniform service. If there are to be minority programmes, might they not most efficiently be centred on the large cities? And might not there be advantages in arrangements which allow, say, 90 per cent of the British population to have access to six choices of broadcast programmes even if the remaining 10 per cent were compelled to put up with fewer than four? As things are, there is certainly no prospect that broadcast television will be able to offer the British public anything like the diversity of programmes which is certain to be commonplace elsewhere by the end of the century.

Another uncertainty in the pattern of broadcasting in the late 1970s is the extent to which the British government will actively encourage the development of cable television. Although some parts of the country, especially in hilly regions where television signals are not easily received, are well provided with cable services, the Ministry of Posts and Telecommunications has not made up its mind about the future of multi-channel cable television. By all accounts, it is waiting for Sir Robert Cockburn's Television Advisory Committee. The difficulty is not merely to know who should be responsible for laying and for financing urban networks of coaxial cables, but also that of deciding who should have access to broadcasting stations linked with them. The ideal is that the maintenance and operation of the cable system should be separated from the right or responsibility to provide programmes. Moreover, there is every reason why the same separation should be made between the technology of television transmission and the provision of programme material. In other words, there is something to be said for putting the BBC on the same footing as the commercial broadcasting companies, for whom the ITA provides central engineering services. Whether one public authority could broadcast television signals and operate coaxial cable networks is a more tricky question. Until that and related problems are answered, however, it is hard to see how any government could make a sensible decision on the future of British broadcasting.

For the British Government, the problems occasioned by the need to provide a more rational basis for broadcasting in Britain touch several parts of the government machine. One important issue to be decided is whether the Post Office should retain its monopoly on the provision of telecommunications links within the country—as things are, even the networking arrangements by means of which the commercial television companies and the BBC transmit from one point to another are owned or at least licensed by the Post Office. There have been circumstances in which television relay companies have been allowed to set up their own arrangements for distributing signals, but it remains to be decided who, if anybody, would be able to operate a network of coaxial cables designed not merely so as to distribute television signals but also the other signals which might profitably accom-

pany ordinary television signals. After all, in due course there is every reason why the same cable network should be used for television transmission and even such urban refinements as burglar alarms and the like. Obviously the separation of such a system from the Post Office would thoroughly undermine the basis on which telecommunications in Britain are at present organized. That would mean too much disruption, but there is no doubt that the Post Office itself is slow to recognize the benefits that could come from a vigorous exploitation of a coaxial cable network for distributing video signals. At least one outcome of the present concern for the reorganization of broadcasting services should be an explicit set of marching orders for the Post Office, which must be made to act more quickly than in the recent past.

100 Years Ago



"University of London, Burlington Gardens, W.,
December 5th, 1871.

"MY DEAR TYNDALL,—If I correctly apprehended what you said at the Dinner of the Royal Society in regard to Dr. Mayer, you repeated what you had previously stated in your Lecture at the Royal Institution in 1863, as to the entire ignorance of Mayer's work which prevailed in this country until you brought it into notice on that occasion.

"Now, I very distinctly remember that a few days previously to that Lecture, I mentioned to you that as far back as 1851 I had become acquainted, through the late Dr. Baly, with one of Dr. Mayer's earlier publications; and that, in bringing before the readers of the *British and Foreign Medical Review* (of which I was then the Editor) the 'Correlation' doctrine, as developed in Physics by Grove, and in Physiology by myself, I had stated that we had both been to a great extent anticipated by Mayer—as I should have shown much more fully if the pamphlet had earlier come into my hands.

"I also most distinctly remember that, as you stated in that Lecture, no one in this country—not even Sir Henry Holland, who knows everything—had ever heard of Mayer, I spoke to you again on the subject a few days afterwards; and that you then expressed your regret at having entirely forgotten what had previously passed between us on the subject.

"As it would seem that this second mention of the matter has also passed from your mind, I shall be obliged by your looking at the passages I have marked in pp. 227 and 237 of the accompanying volume, from which I think that you will be satisfied that I had at that date correctly apprehended Mayer's fundamental idea, and that I have done the best to put it before the public that I could under the circumstances—the article having been in type and ready for press before his pamphlet came into my hands.

"Since, in thus bringing forward Mayer, I spontaneously abdicated the position to which I had previously believed myself entitled, of having been the first to put forward the idea that all the manifestations of Force exhibited by a living organism have their source *ab extra*, and not—as taught by physiologists up to that time—*ab intra*, I venture to hope that you will do me the justice of stating the real facts of the case in a short communication either to the *Athenæum* or to *NATURE*.—I remain, my dear Tyndall, yours faithfully,
"WILLIAM B. CARPENTER
"Prof. Tyndall."

From *Nature*, 5, 143, December 21, 1871

OLD WORLD

ESRO

Italians Frustrated

IN spite of all the entreaties of recent weeks and a last ditch offer by the Italian government, Esro decided last week that it would stop supporting the present scientific activities at the European Space Research Institute (Esrin) at Frascati, Italy, after September 1973. The door is not completely closed, however, and as a sop to the scientists and others that have been fighting hard to keep Esro as a viable scientific entity the Esro council suggests that "additional Esro activities appropriate to location at Frascati are to be investigated in cooperation with the Italian authorities".

It now remains to be seen whether the Italians carry out their threat (see *Nature*, 234, 3; 1971) to withdraw from Esro as their plan for an Esro/Centro Nazionale delle Ricerche (CNR) collaboration has not been accepted by the council. According to this plan Esro was to have contributed \$1 million a year towards the cost of running the laboratory while the Italian government would have contributed \$1.7 million. It became apparent two weeks ago at a previous Esro council meeting that this plan would have a rough passage when two member countries—Germany and the Netherlands—expressed concern over the \$2.0 million a year that Esro is currently costing Esro—this being a different objection to that first voiced against the continued support of Esro, namely that the research carried out at the laboratory is not compatible with the future aims of Esro.

Esro still plans to use the buildings at Frascati and it was announced last week that the Esro technology dissemination service is to be transferred from Paris to Frascati in late 1972 or early 1973. Such a move is not likely to placate the Italians as their aim is to keep a viable Esro scientific effort within Italy.

As well as stopping support for Esro the Esro council agreed that as from next July the organization's sounding rocket launching range at Kiruna in Sweden would be transferred to the Swedish authorities. These decisions will lead to employment problems for Esro and, although most of the employees at Kiruna will become employees of the Swedish government, it is far from clear what will become of the employees at Esro—75 of whom are scientists. Esro currently employs 1,300 people—120 of whom are graduate scientists, 365 graduate engineers, 475 technicians and 340 administrative and other personnel. It is not known at present how the decisions will affect the number of employees although an Esro spokesman said last

week "there is certainly no mass redundancy of any kind being planned".

The Esro council also agreed at last week's meeting on an overall plan for the organization until 1980. There will be an intensification of the applications satellite programme that will receive \$70 million a year during 1974–80. Activities during the next few years will be concentrated on prototype development of aeronautical, navigation, meteorological and technological satellites and the budget during 1972–74 will be maintained at \$283.6 million which will increase to \$330 million during 1975–77.

MARS

No Cause for Concern

from our Soviet Correspondent

THE successful soft-landing on Mars, at a point approximately 45° S, 158° W—between the Electris and Phaethontis regions—of the instrument capsule from the Mars-3 probe has led to concern among some western observers about the possibility of biological contamination of the planet. The veil of secrecy surrounding the Soviet space programme has not helped to allay this disquiet, nor has the absence of any mention of biological experiments aboard the current probes in the preliminary press reports.

Writing in *Pravda* on December 6 (after the first batch of data and the short-lived video signals from the Martian surface had been received by orbital relay), Dr L. Mukhtin, Head of the Departmental Laboratory of Exobiology of the Institute of Space Research of the Soviet Academy of Sciences, stressed that exobiology is still part of the Soviet Mars programme. The search for life and for organic compounds, whether of biological origin or produced by ultraviolet radiation, will be carried out by future probes using "specially developed automata". The current probes, he says, are only "preparing the ground" for this important survey. If the results are negative, and "a strict proof of the absence of life on Mars" is obtained, this will be of equal scientific importance, "giving the possibility in the future of carrying out biological experiments in the conditions of a completely sterile planet".

It seems clear, therefore, that the Soviet Laboratory of Exobiology considers the Mars-3 descent capsule not to be a biological hazard to the planet.

CHEMICAL INDUSTRY

Dow Europe Healthy

DOW EUROPE, a subsidiary of the Dow Chemical Company, is now one of the most profitable members of the Dow group. Since its creation in the early 1950s to provide the European and African markets with specialist products (agricultural chemicals, for example) it has evolved in such a way that it now accounts for 26 per cent of Dow's world sales (which are at present running at \$2,050 million a year) and about 30 per cent of the company's profits.

The president of Dow Europe, Mr Z. Merszei, claims that the goal set in 1963 of a 10 per cent increase in earnings each year has only been missed once—in 1970. And he says that the financial results for 1971 will show that the rate of growth of profits has clearly recovered to its pre-1970 level. The financial director, Mr P. Stroebel, says that the increasing growth of the company at a time when others are tightening their belts is a consequence of fundamentally different attitudes within the Dow corporation. Although many companies direct their investment to increasing their share of well tried markets, he said, Dow was always trying to tap new ones. Dow's European showpiece, its plant at Stade, West Germany, will soon be the company's largest chemical complex in Europe, producing many of its basic chemical requirements such as chlorine and sodium hydroxide.

Over the years Dow has channelled about 6 per cent of its European investment into Britain where there are now two manufacturing plants, at Barry and King's Lynn. The company also recently announced the establishment at King's Lynn of an agricultural research centre at which thirty professional scientists will eventually work; its budget is expected to be about \$1 million a year. Dow already has what are described as technical service laboratories at Horgen, Switzerland, but the King's Lynn centre will be the company's first fully fledged research laboratory in Europe.

INDUSTRIAL RELATIONS

Same Game, New Rules

C. A. PARSONS, the Newcastle engineering company, has once again issued dismissal notices to 33 employees who are members of the United Kingdom Association of Professional Engineers. The company originally dismissed the engineers last July when they refused to join the Draughtsmen's and Allied Technicians' Association which, by working to rule twice and striking once,

won a closed shop agreement from Parsons in May 1970.

Mr Jack Hill, the most senior of the 38 engineers then involved, sued Parsons for wrongful dismissal and last month the Appeal Court declared in his favour. Mr Hill and UKAPE regarded it as a test case, but last week Parsons issued the new dismissal notices to the remaining engineers with periods of notice ranging from three to six months according to length of service. At the same time, new contracts were offered which include the taking up of membership of the AUEW—with which DATA has now merged—as a condition of employment.

UKAPE's reaction has been to apply to the newly established Industrial Relations Court for a sole bargaining agency on behalf of the engineers at Parsons. This means that the resolution of the dispute awaits the decision of the court some time next year. UKAPE is the first union to apply to the Industrial Relations Court, and the decision will be one of the first under the new law. The fact that UKAPE is a registered trade union under the Industrial Relations Act, while AUEW has deregistered, only complicates the issue.

The only comment that DATA and Parsons were prepared to make this week on the new dismissal notices is that they are honouring the closed shop that they both agreed to last year.

METEOROLOGY

Typhoon Troubles

from a Correspondent

ONE of the most absorbing lectures delivered at the Unesco seminar on the effect of wind on building and structure, held on November 22–26 at Manila, Philippines, was by Professor Sean

Mackey, University of Hong Kong. He discussed work on a ten storey building on Hong Kong island that has recently been built specially to study the effects of strong winds—in particular typhoons—on tall structures. The building, at Cape D'Aguilar, faces the sea and is particularly open towards the north-east from where the strongest winds blow when typhoons approach Hong Kong. So far only one such storm has occurred since the trials commenced and although this particular typhoon did not produce wind speeds of more than 100 mph other storms in Hong Kong have given gusts up to nearly 150 mph.

The building, as shown in Fig. 1, is 100 foot tall and of exposed structural steel construction. The floors are made partly of reinforced concrete solid-slab construction and partly of composite construction with a solid-reinforced concrete slab roof. The building can be divided into four sections, each coupled together at every floor level so that in strong winds the whole building acts as one unit.

On the right of Fig. 1 can be seen the four 175 foot high towers upon which a total of 44 anemometers have been fixed—one at each of eleven different levels on each tower, which are situated about 200 foot to the north-east of the building. To the left of the four main towers can be seen two additional masts, forty foot high, upon which are installed a further six anemometers to measure turbulence decay between the main recording point and the nearest building face. The white spots on the building face shown in Fig. 1 are several of a total of 102 pressure cells mounted in the glass wall panels. Special electro optical tracking instruments together with seismometers are also used to record sway and vibration characteristics of the building.

Although it is too early yet to assess results of actual typhoon winds the experiment and the Unesco seminar have drawn together meteorologists, architects, engineers and the building industry in an effort to draw attention to the urgent need to construct safe buildings which will stand up to the devastating effects of storm winds in typhoon prone areas.

EUROPEAN UNIVERSITIES

Common Problems

TEACHING ability should be taken into account when academics are considered for promotion, and inducements should be offered to them to ensure that they teach well. This was one of the themes that emerged from the Conference of European Rectors in Copenhagen last month, when representatives from the universities of twenty-five countries met to discuss the teaching role of the university.

Dr Albert Sloman, Vice-Chancellor of Essex University and president of the conference, said last week that he felt that all European universities are facing basically the same problems, but that they have reached them by different routes and therefore they might have to produce different solutions. For example, the call from university appointments officers and employers in Britain for more relevant courses is even louder in France where open access to university—as opposed to the selective access in Britain's universities—means that vast numbers of students are obtaining qualifications, particularly in the humanities and the social sciences, which are comparatively worthless as the staff-student relationship is too great for them to be well taught and the courses themselves are no real qualification for a job.

The conference, which has been meeting at six monthly intervals since Dr Sloman became president in 1969, is not an executive body, but simply meets for the rectors to exchange views; opinions differed most over the future role of universities. In his concluding remarks Dr Sloman suggested that it is very doubtful if society, with the cost of higher education rising, will allow every teacher the opportunity for substantial research. This could produce two types of institution—one heavily inclined to research and the other to teaching—as in Britain where both universities and colleges of technology and education exist. Alternatively there might be a single institution with people specializing in either teaching or research. Whichever is adopted Dr Sloman for one feels that there must be greater mobility of staff between research and teaching, as research should enrich teaching and teaching should enrich research.



Fig. 1 General view of the testing site from the south-east

NEW WORLD

Rogers Campaign Conquers Congress

by our Washington Correspondent

AFTER nearly a year of debate, with some of the most intensive lobbying ever devoted to scientific research, Congress has finally decided on a plan for organizing cancer research in the United States. President Nixon is said to be happy with the legislation and ready to sign it into law, thereby putting an end to a remarkable series of policy reversals by the Administration and making available \$1,600 million for cancer research in the next three years.

One of the most remarkable aspects of the affair is that the debate has been almost exclusively concerned with the organization of cancer research. Throughout the long debate, it has been tacitly assumed that any amount of money can be spent wisely, and that there are many good ideas crying out for money to be put into effect.

The legislation now passed is substantially the same as the bill introduced into the House of Representatives by Congressman Paul G. Rogers in September, for whom the outcome of the debate is a great personal victory. As recently as July, it seemed that the support of Senator Edward M. Kennedy and President Nixon for a bill designed to make cancer research virtually independent of the National Institutes of Health would be strong enough to carry the bill through the House of Representatives. Only during the hearings held by Rogers's subcommittee was the biomedical community able to voice its fears about the dangers of such a measure.

Rogers's bill gained considerable congressional support in spite of powerful lobbying for the Senate bill by the American Cancer Society and by lobbyists connected with Mrs Mary Lasker, a New York millionairess and philanthropist who has in the past been instrumental in persuading Congress to increase appropriations for health research. The bill has survived his committee and the House of Representatives with only a few minor changes. More important, Mr Rogers has managed to keep nearly all his proposals in a conference committee set to iron out the differences in House and Senate passed bills.

As reported out of the conference committee and passed by Congress last week, the chief elements of the legislation are as follows.

The National Cancer Institute will coordinate all of the activities of NIH related to cancer, and it will remain

functionally a part of the NIH. The Senate bill would have established a Conquest of Cancer Agency virtually independent of NIH.

The National Cancer Institute's budget will each year be submitted directly to the President, with opportunity for comment by the chairman of the National Cancer Advisory Board and by the Director of the National Institutes of Health. This measure, which is the same as that contained in the House bill, will give the National Cancer Institute some autonomy, and should ensure that its budget is kept at a high level.

A three man board will be set up to monitor the progress of cancer research, and to keep the President informed of any delays or blockages in funding or other bureaucratic difficulties that hold up research. The panel will be composed of three people who "by virtue of their training, experience and background are exceptionally qualified to appraise the National Cancer Program". Rogers managed to resist efforts in the conference committee to restrict the membership of the panel to the Director of NIH, the chairman of the National Cancer Board and the Director of the National Cancer Institute, although there seems to be some disagreement about whether those individuals would still be eligible to be members of the panel. If so, that would put them in the peculiar position of monitoring a programme for which they are responsible.

The legislation sets up fifteen new cancer research centres funded by block grants from the National Cancer Institute. Existing centres would also be able to receive block grants for research, and individual grants of less than \$35,000 could be awarded by the Director of the National Cancer Institute on the basis of peer review, without first seeking the approval of the National Cancer Advisory Board.

A national Cancer Advisory Board will replace the present National Cancer Advisory Council. This is the only major provision contained in the Senate bill that survived the conference committee, and its effect will be to make the advisory body slightly more political. As at present constituted, the National Cancer Advisory Council consists chiefly of scientists and physicians appointed by the Secretary of Health, Education and Welfare, but the new legislation sets up a board con-

sisting of twenty-three members appointed by the President. *Ex-officio* members would be the Secretary of Health, Education and Welfare, the Director of the Office of Science and Technology, the Director of NIH, the chief medical officer of the Veterans Administration and a medical officer designated by the Secretary of Defense, and the remainder of the places would be divided among scientists and laymen in the ratio of two to one. Apart from advising on overall policy for the National Cancer Program, the board will provide a report for the President and Congress each year on the progress of the programme.

One interesting aspect of the workings of the new bill will be the interplay between the National Cancer Advisory Board and the President's Cancer Panel, both of which are charged with the task of overseeing the cancer programme and both of which are essentially political bodies. Their relationship to each other is at present unclear, but there is bound to be some overlap.

SICKLE CELL ANAEMIA

Senate Prescription

by our Washington Correspondent

HAVING decided how to organize cancer research, Congress is now turning its attention to sickle cell anaemia—another disease ripe for an injection of Federal funds. Last week, the Senate decided to give \$142 million over the next three years to programmes designed to combat the debilitating effects of the disease through research, and treatment, and to genetic screening and counselling aimed at cutting down the frequency with which it occurs. The Senate's deliberations on the legislation were marked by uncharacteristic alacrity, for the bill was passed only two months after it was first introduced by Senator John V. Tunney of California (see *Nature*, **233**, 517; 1971).

The disease is believed to afflict some 50,000 Americans, almost all of them black. Sickle-cell anaemia is the product of a recessive gene, which means that only homozygotes are frankly affected. Carriers of the sickle-cell trait, heterozygotes, are, however, partly protected against malaria, which explains the frequency of the gene among the descendants of the West African negroes in the United States. Some 2.5 million people carry the recessive sickle cell

gene. The Senate's programme is therefore directed principally towards setting up genetic screening and counselling centres to identify couples whose children may be at risk, and another important part of the legislation is the provision of \$42 million over the next three years to support research into the diagnosis, treatment and control of the disease.

Senator Edward M. Kennedy's public health subcommittee, which handled the legislation, was evidently impressed by witnesses who described the results of treating sufferers of sickle cell anaemia with urea or cyanate compounds. Such treatment is essentially aimed at overcoming the so-called sickle cell crisis—the painful and debilitating symptom of the disease caused when the red blood cells lack oxygen and form themselves into the sickle shape, severely restricting the flow of blood to tissues—but it is the subject of heated debate among many physicians. The committee report talks of a possible breakthrough in this area, and the bill authorizes the Department of Health, Education and Welfare to spend \$5 million on research in 1973, \$10 million in 1974 and \$15 million in 1975.

Since the cause of the disease is genetic, it is incurable (in spite of a curious phrase which crept into the committee report to the effect that "further work in the field of genetic engineering also offers scope in the struggle to conquer this crippling malady"), and the Senate's bill therefore lays considerable emphasis on the provision of screening and genetic counselling centres to pinpoint carriers of the sickle cell trait and to advise couples who both carry the trait of the risks of bearing children who have the disease. Kennedy's subcommittee in fact increased the provision for setting up such clinics by the Department of Health, Education and Welfare by bumping up the funding to \$25 million in 1973, \$30 million and \$40 million in 1975, chiefly on the basis that it would cost about \$60 million to establish only ten such centres.

The bill also sees a role for the Department of Defense and the Veterans Administration in the fight against sickle cell anaemia, authorizing the defence department to conduct a screening programme, and giving the Veterans Administration a total of \$12 million over the next three years for research.

If a similar bill is passed by the House — companion legislation was introduced by the District of Columbia delegate Walter Faunteroy and Mr Paul G. Rogers's health subcommittee has already conducted hearings on the bill — the Administration could be put in something of an embarrassing position. It was President Nixon who set the ball rolling in his health message to Congress last February, when he referred to the

"shameful fact that the causes of this disease have been largely neglected throughout our history", but the bill that he is now likely to get back from Congress will contain expenditures many times greater than the present \$6 million a year that is devoted to research, treatment, screening and counselling. Since there have already been many charges that the disease has been neglected because it is confined chiefly to blacks, the Administration would find it very difficult to oppose the legislation, even though Nixon now seems to enjoy testing his muscle with Congress over all sorts of legislation.

Short Notes

Ocean Dumping

THE Senate agreed recently, by a vote of 73 to 0, to a bill designed to prohibit unregulated dumping of wastes into the oceans around the United States. The bill is in most respects the same as that passed in September by the House of Representatives, except that a provision designed to set up marine sanctuaries in some ocean areas has been removed. The designation of marine sanctuaries was intended by the House of Representatives to preserve intact areas of ocean for ecological, recreational or aesthetic reasons, and it would have led to the control of activities such as oil drilling in the designated regions. The provision was opposed in the Senate because the sanctuaries would have been set up in international waters—a suggestion to which senators objected because it may violate international law and also it may be viewed by other countries as "creeping jurisdiction" over areas of the high seas. The Administration also opposed that part of the House bill because it would have cost about \$10 million to institute.

Nutrition

WHEN Dr Robert B. Choate, a nutrition consultant, told a Senate Committee last year that many leading brands of breakfast cereal are over-advertised and under-nutritious, his revelations were greeted with scorn from the multi-million dollar industry (see *Nature*, 227, 548; 1970). Nevertheless, while trying to belittle Mr Choate's analyses, the industry has been busy reformulating its products, and Mr Choate recently published a revised chart showing that twenty-six of the previously non-nutritious products have been considerably fortified with nutrients. Two of the most heavily advertised brands—Kellogg's Corn Flakes and Kellogg's Rice Krispies—are, however, among the bottom 10 per cent of all breakfast products in nutrient value, and on Mr Choate's analysis, can still be considered as "empty calories". The Food

and Drug Administration has been developing nutrient guidelines for cereals for the past eighteen months, but "industry pressure and the lassitude of academia make us wonder whether the Food and Drug Administration will ever establish nutrition guidelines which can serve as a basis for ethical advertising slogans", Mr Choate tartly remarked.

Shuttle

A SERIES of meetings was held recently between officials of NASA and the European Space Conference to discuss possible areas for cooperation on the post-Apollo space programme. The meeting is said to have produced a list of projects on which Europe and the United States may be able to cooperate. They include major responsibility for development of the space tug, subsystems of the shuttle and supporting studies in related technology areas. It is now up to members of the European Space Conference to select specific projects on which to cooperate, and another meeting has been fixed for February for further discussions.

AEC and the Environment

PROPOSED amendments to the Atomic Energy Commission's regulatory procedure, published in the Federal Register recently, further extend the agency's control over the environmental consequences of building nuclear power plants. The AEC is intending to prohibit the clearing of land and other site preparations, such as construction of non-nuclear facilities such as turbine buildings, until a construction permit has been issued. The chief effect of the new regulations, which are at present open to public comment, would be to make such activities a part of the review of the environmental impact of a proposed plant.

Arms Race

THE Federation of American Scientists, a consistent and vocal critic of the arms race, last week proposed that the President of the United States must have the approval of Congress before unleashing nuclear weapons in a first strike situation. The federation, which has always been opposed to the first use of nuclear weapons, has proposed this policy in conjunction with the War Powers Act introduced into Congress recently by Senators Javits, Stennis and Eagleton. The federation believes that such an arrangement would have the advantage of building into the nuclear arsenal an extra safeguard, and it would also have the added advantage of reducing international tensions during crises such as the Cuban missile crisis, since the first use of nuclear weapons by the United States would be ruled out unless Congress had given its express approval.

Preparation for a Rumpus

In the next few weeks *Nature* will publish a series of comments on the Dainton and Rothschild reports recently published in *A Framework for Government Research and Development*. The first is by Professor M. Swann, Principal and Vice-Chancellor of the University of Edinburgh.

THESE two reports make a fascinating contrast: Rothschild, on the one hand, wearing a loud check, thumps everybody and everything in sight and hurls around vulgar, academically disagreeable phrases like the "customer/contractor principle", in staccato fire. Dainton, on the other hand, in a well-cut, dark suit, analyses soberly and reasonably the troubles of a piece of the scientific establishment, in tones reminiscent of a professional man to his well-to-do client. No wonder there is going to be a rumpus.

In the light of the extensive leakages that have been seeping round the scientific world in recent months, I was certain that I was going to be a staunch Daintonite. Now that I have read the reports, and thought about them, albeit for not as long as I would like, I confess to thinking that the path of true wisdom for the well-being of science and society in Britain, lies somewhere midway between the two—perhaps even a little nearer Rothschild than Dainton. I don't expect this to be a popular point of view in academic circles.

One should not, of course, speak of the research councils in the plural. They vary enormously. NERC has been going for so short a time that one can only say it has made a good start with a difficult and diverse team. The ARC on the other hand, while it has indeed paid for itself many times over with Proctor Barley and other things, has been inviting trouble by failing in large measure to help and encourage agricultural and veterinary research in universities, and preferring to set up large specialist institutes which simply ask to be taken over by ministries. Ironically, Rothschild himself was once chairman of the ARC.

The real reputation of research councils rests on the achievements of the MRC and more recently the SRC. These are deeply impressive, and are envied and imitated the world over. These structures must not be dismantled. But (and having served on both councils, I know) their policies, by the very nature of their structure, are determined far more by the interests

and demands of academic research workers than by the needs of society. There is no harm and on the contrary much good in this. Scientists know where science is going, in a way that ministries and society do not. Research councils can, and do, present society with benefits that no customer would ever have thought to ask for from his contractor.

It does mean, however, that research councils, concerned, as laid down in their charters and as their structures ensure, to support research of timeliness and promise, find great difficulty in stimulating work that meets some immediate social need but fails to attract good research workers. As an example, years ago, when I was on the MRC, some of us were concerned to stimulate more dental research (then, as now, slender), on the grounds that dental treatment cost the nation some hundreds of millions of pounds. We failed, I fear, to make any impact on the problem, and I am not aware that our successors have been markedly more successful. Given the research council structure, these are intractable problems not to be solved simply by the optimistic policy-making of a restructured Council for Scientific Policy.

Turning to Rothschild, I think it is unfortunate that he has put forward his proposals at a time of financial stringency and that he has put all his emphasis on the customer/contractor relationship, which I believe to be, in reality, the secondary consequence of a much more fundamental and acceptable reform that he proposes.

Had times been less hard, so that he could have left the research council budgets intact, I doubt if the academic/research council world would have objected to what he proposes. On the grounds that it would have meant more science, and more power for scientists, they would probably have welcomed it. It is not his fault that things have turned out otherwise. We have to accept at this moment a total science budget that is all but static.

My second criticism, however, is Rothschild's fault—in his presentation. I believe that his real contribution is to

propose a structure, spreading through most if not all the departments of government, that builds in scientists, not in some pallid backroom advisory capacity, but in positions of influence.

This cannot be achieved, however, unless the departmental scientists can themselves call for research that will solve the departmental problems. And this in turn implies something like the customer/contractor relationship.

In another way, if we adhere too closely and universally to a research council structure that was expressly (and for good reason) designed to keep science and the scientists detached from the governmental structure, we can hardly be surprised that the governmental structure remains detached from the scientists. Rothschild wants to alter this, and he is right. But we must see that the civil servants do not, wittingly or unwittingly, torpedo his good intentions. Then we should have the worst of every world.

While I accept that some transference of research council budgets to ministries is essential, in a time of financial stringency I am concerned that the transfers should not be such as to shatter the research council structure, which undoubtedly, is far too valuable to lose. Moreover, if it is right that there be a 10 per cent surcharge on contracts for basic work, as I am sure it is, then it is surely also right that research councils be encouraged and allowed to do applied work on their own initiative. They may, after all, see the problems more clearly, and commission the work more skilfully themselves. I suggest, therefore, that the transition be decidedly more cautious, and initially smaller than Rothschild allows.

To sum up, I can do no better than say that the Green Paper recalls vividly the days when I and others, before our paths diverged, used to collaborate in research with Rothschild, on the mechanisms of fertilization in the sea-urchin egg. This was a hilarious business, conducted in marine biological stations around the world, and involving much noisy argument. It resulted in quite a lot of joint scientific papers. Sometimes one of us wrote the first draft and sometimes Rothschild did, in a style indistinguishable from his current report (doubters may care to look at his book on fertilization). In the latter event, even more noisy argument was needed to convert his first draft into a smooth acceptable manuscript. But we liked to think that the end results were good. And so perhaps they could be on this occasion.

NEWS AND VIEWS

Networks in Nature

THE use of analogy has for so long been part of the fabric of scientific method that the degree to which the very language of natural law is imbued with half-assimilated references of a historic or picturesque nature is apt to be forgotten. Sometimes the allusion is hardly more than metaphorical, sometimes it is completely misconceived; occasionally it embodies logical interrelationships of an extremely penetrating kind. In theoretical physics, where perhaps formal analogies stand out more clearly than elsewhere, their exploitation can be a matter of considerable subtlety, for a similarity between the equations governing experimentally separate phenomena can sometimes extend deeply into the more yielding sub-structure of hypothesis and thought experiment which lies beneath them. A careful study of this kind of interrelationship may then lead to insights into both fields which would hardly have been possible were they to be treated in isolation.

One of the most striking and fruitful of all interdisciplinary analogies—that between electrical networks and thermodynamic systems—has been the subject of increasing activity in recent years and is treated in an extensive article by Oster, Perelson and Katchalsky in this issue of *Nature* (page 393). Although “equivalent circuit” representations of macroscopic mechanical and microscopic acoustic and rheological systems have been utilized for many years—not least in the analogue computer—this aspect, though of practical importance, touches only superficially the heart of the matter. The deeper level, at which one considers the nature of the dissipative process in circuit elements, the interplay between reversible (reactive) and irreversible (resistive) energy flows, the symmetry of input and output and so on, has only been examined in comparatively recent times and this largely due to the work of a single man, Josef Meixner in Aachen.

When Meixner, some ten years ago, began his reappraisal of the connexion between thermodynamics and network theory (*J. Math. Phys.*, **4**, 154; 1963), little was appreciated—beyond certain themes which could be traced back to Maxwell, Kelvin and Heaviside—of the precise way in which each of these considerable bodies of knowledge held implications for the other. Even now it is necessary to caution the reader conditioned by classical heat theory that an electrical network exchanging energy with its surroundings is a thermodynamic system in its own right, so that its treatment is more by extension of than analogy with conventional results. Meixner's findings, which were also relevant to distributed parameter systems and electric fields (*Acta Physica Polonica*, **28**, 113; 1965), proved to be far more than textbook curiosities, for, in addition to providing particularly transparent examples of the essential identity of the Onsager-Casimir reciprocal relations of classical non-equilibrium thermodynamics and the reciprocity of the admittance matrix for networks, they led eventually to a fundamental reconsideration of the usefulness of the concept of entropy in non-equilibrium physics.

The central feature of Meixner's approach is the con-

cept of “passivity” in a system and the importance of this is reasserted by Oster, Perelson and Katchalsky in the related language of Tellegen's theorem for networks. Though at first sight the passivity property seems to be simply an expression of energy conservation in a system without sources, it can be shown to imply deeper stability conditions and thus connect with the second as well as the first law of thermodynamics. By bringing to bear the now well-developed apparatus of generalized network theory, Katchalsky and his colleagues have been able to point the way to a number of extensions of the Aachen formulation which promise considerable advances in both practical and theoretical terms.

First, Katchalsky and his colleagues show, with examples from membrane systems, how the techniques developed in engineering systems theory might be applied to the extremely highly connected and inhomogeneous patterns of forces and fluxes which are characteristic of cell biology. For this they introduce an element unfamiliar in physico-chemical thermodynamics—the idealized “transducer”, a transformer-like unit with possibly non-linear response. They also explain how some of the graphical techniques developed by engineers can enormously simplify the writing of network equations, emphasizing, however, that a good diagrammatic notation can be far more than a book-keeping scheme or an algorithm for recovering these. As in other branches of physics, diagrams may here provide a calligraphy, so to speak, for the topological relations embodied in the connectedness of the system, properties which may be obscured in the bare equations themselves.

The results of Oster, Perelson and Katchalsky are by no means limited to prescriptions for codifying network structure in physico-chemical systems; in fact they emphasize two further aspects which seem to go significantly beyond the established concepts of non-equilibrium thermodynamics. They accept the inevitability of non-linear constitutive relations, which have always been shunned by physicists, showing how these can be accommodated, at least formally, in a Hamiltonian-like system related to the so-called Brayton-Moser equations for networks, and, in what seems to be a major step, explain how the reciprocity properties of networks—which in electrical terms refer literally to interchange of input and output—can be taken over into thermodynamics to give a non-linear generalization of the Onsager-Casimir reciprocal relations. For non-linear passive systems the key quantity in this turns out to be the Jacobian of the force-flux transformation, which in turn implies an integrability condition and the existence of state functions such as internal energy.

As the authors are at pains to point out, even such sophisticated treatments remain phenomenological in character, in network theory just as in conventional thermodynamics. One must still put in not only the parameters of the system and the forms of the constitutive relations governing the junctions, but, in practice, also make implied postulates about the level at which system elements are known in structural detail and below which

they appear simply as "black boxes".

It is in this aspect that the doubts raised by Meixner about the usefulness of "entropy" as a function to characterize macroscopic non-equilibrium systems arise. His conclusion is quite unequivocal: "Unsere Behauptung ist nun, dass die Definition einer eindeutigen Entropie für Vorgänge nicht nur bisher nicht geschehen sondern sogar unmöglich ist, falls man nur makrophysikalische Überlegungen zulässt, d.h. die Existenz der atomistischen Struktur der Materie ignoriert." ("Our assertion is thus, that the definition of an unambiguous entropy for (non-equilibrium) processes not only has not so far been achieved but is actually impossible, so long as only macroscopic considerations are admitted, i.e. the existence of an atomic structure of matter is ignored.") (*Rheologica Acta*, 7, 8; 1968.)

Although such a conclusion is strongly suggested by statistical mechanics Meixner's conviction is based on the disarmingly simple observation that a two-terminal resistive network can be reproduced—so far as its input-output characteristics are concerned—by an infinite variety of equivalent "black boxes" containing inductances and capacities. Because these can never be distinguished without some process of opening the boxes and examining their internal structure, neither can the irreversible (resistive) dissipation of energy be properly separated from the reversible (reactive) energy flow. By the same token the dissipative processes in thermodynamics cannot be unequivocally characterized, except at a sub-microscopic level, in fact only at the point where the continuum approach must give way to an atomistic statistical mechanics.

Thus macroscopic thermodynamics comes up against something like the information-theoretic barriers which are accepted, in somewhat better grace, by the users of black-box formulations in behavioural psychology and automata theory. Meixner has shown that the consequences of this are not irreparable and that an entropy-free thermodynamics may be constructed, at least for linear systems, using the passivity principle. It now seems reasonable to hope that the advances described by Katchalsky, Oster and Perelson may point the way to a similar development for non-linear thermodynamics before long.

Muscling In

MOTILITY, the ability to move, is one of that list of characteristics of living organisms which every schoolboy learns, or used to have to learn, by rote in his first biology lesson. Cells and other organisms exhibit movement at some stage or in some part during their life history and, perhaps not surprisingly, evidence is steadily accumulating which suggests that motility and contraction in many, indeed perhaps even in all biological systems, has a common molecular basis.

Striated skeletal muscle of animals is, of course, the classic, most accessible and most thoroughly analysed contractile apparatus of organisms. It now seems beyond dispute that muscular contraction depends on the interaction of polymers of two contractile proteins, actin and myosin, which are arranged in interdigitating arrays of filaments. At least, when a striated muscle contracts projections from the myosin filaments cyclically attach to, and detach from, adjacent actin filaments in such a way that transient actomyosin bridges pull the actin filaments into the myosin filaments with the net result that the muscle shortens.

Armed with the knowledge that actin and myosin comprise the basic contractile machinery of muscles, biologists have, naturally enough, repeatedly searched for either or both of these proteins in other tissues, cells and organelles which move. And as the techniques for extracting and characterizing proteins have improved actin-like and myosin-like proteins have, sure enough, been identified with increasing frequency and certainty in all sorts of situations.

A few weeks ago, for example, Fine and Bray reported in *Nature New Biology* (234, 115; 1971) that as much as about 20 per cent of the total protein in chick neurones is an actin-like protein, which may very well be identical to skeletal muscle actin. They also find actin or actin-like proteins in chick embryonic lens, lung, skin, heart, pancreas, kidney and brain tissue. And in this issue of *Nature* (see page 410) Gawadi reports the location of actin which has been observed in the mitotic spindle apparatus; he believes it occurs in filaments running parallel to the long axis of the spindle but not closely associated with the spindle micro-

tubules. Behnke, Forer and Emmeresen (see page 408) reach much the same conclusion about the distribution of actin or actin-like protein in the meiotic spindle of crane fly spermatids and they also report the presence of this muscle protein in crane fly sperm tails. Other workers have claimed to detect actin or myosin-like proteins in mitochondria, chloroplasts and cilia and, recently, Adelstein, Pollard and Kuehl (*Proc. US Nat. Acad. Sci.*, 68, 2703; 1971) report isolating both actin and myosin-like proteins from thrombosthenin, the complex of contractile proteins in human blood platelets; these examples by no means exhaust the list.

It has to be admitted, of course, that more often than not the criteria for the identification of these two proteins in novel situations are not rigorous enough to satisfy completely the standards set by muscle biochemists. But where serious attempts have been made to compare skeletal muscle actin and actin-like proteins from other sources—the experiments of Fine and Bray are a case in point—few differences have been detected, although, as Fine and Bray themselves comment, nothing short of the total amino-acid sequences of actins from different sources can establish their complete identity or the extent of differences. That proviso notwithstanding, however, the sweeping generalization that actin and myosin-like proteins may universally provide the molecular basis of motility in biological systems becomes almost daily more attractive.

TAXONOMY

Postgraduate Course

FROM next October an MSc course in animal taxonomy will be organized by the Department of Zoology and Applied Taxonomy at Imperial College, London, in collaboration with its neighbour in South Kensington, the British Museum (Natural History). This will be the first postgraduate course devoted specifically to animal taxonomy; it will also be the first linkup between a British national museum and a university department to produce a postgraduate course in the biological sciences.

PRIMATE BEHAVIOUR

Focus on Function

from a Correspondent

USING a previously successful formula, the Primate Society of Great Britain and the Association for the Study of Animal Behaviour joined forces to hold a symposium on primate behaviour on November 25 and 26 at the Zoological Society of London. Three major research areas were covered: field studies of behaviour and ecology; laboratory manipulation of primate behaviour; and human ethology. In all of these areas, it is now clear that research workers have generally progressed beyond mere use of established terminology and the belief that such description constitutes scientific explanation. In most studies, functional relationships now form the focus of research.

Following the example of Dr John Crook (University of Bristol), many field workers are now concentrating on the relations between primate behaviour and the natural environment. This central interest was present in varying extents in contributions on the natural behaviour of the mouse lemur (Dr R. D. Martin, University College, London), the red colobus (Mr T. Clutton-Brock, University of Cambridge), the talapoin (Dr Annie Gautier, University of Rennes), and simian primates in Malayan forest (Dr D. J. Chivers, University of Cambridge). Recent studies demonstrate a clear correlation between general behaviour (particularly social structure) and environmental features such as food availability and food distribution. The precise techniques developed by Mr Clutton-Brock for investigating patterns of home ranges have destroyed the myth that forests are homogeneous areas of trees, and this kind of study will doubtless become increasingly important in the future. The data already available show that spatial and social systems of primates are adapted to key environmental factors in a highly sophisticated fashion. The study by Dr J. C. Rodman (Harvard University) of the orang-utan further brought out the point that many primate species exhibit local variations in social structure and home-range attachment. In Dr Rodman's study area, the orang-utans are sedentary, in contrast to those observed previously by John McKinnon in a different region.

The symposium also included two excellent studies on specific aspects of behaviour which have long required investigation: Dr J. Deag (University of Edinburgh) gave a graphic account of intergroup encounters in wild Barbary macaques, showing that these primates do (after all) exhibit a refined form of territoriality—so refined that a less careful observer might have over-

looked it entirely. Dr M. J. A. Simpson (University of Cambridge), covering a different subject, provided an elegant analysis of male grooming relationships in a wild chimpanzee group. Male chimps spend more time grooming other males than females, and the high-ranking males groom most, although it is the subordinate chimp in any encounter which will groom longest.

The laboratory behaviour manipulators produced some extremely good contributions and there were distinct signs of greater appreciation of "natural behaviour" in these investigations. Dr R. P. Michael (Institute of Psychiatry, London) gave a lucid account of his team's research on hormonal control of sexual activity in female rhesus monkeys and neatly showed the potential calibre of long-term projects. His techniques permit quite detailed analysis of factors operating in mating activity, and one important observation is the occurrence of a point where the hormone-treated, castrated female is attractive to the male, but is not yet "interested" in him. This indirect demonstration of the action of female attractive scents ("pheromones") has been supported by precise studies of female vaginal secretions, including gas chromatographic analysis.

Providing a relief from many castration experiments, Professor D. Ploog (Max-Planck Institute for Psychiatry, Munich) gave an interesting review of communication in captive squirrel monkeys, bringing together various results from behavioural observation, recordings of vocalizations and experiments using cerebral radio-stimulation. The combination of techniques used in this ambitious study is now beginning to provide a detailed picture of the

central nervous control of communication in this species. Professor R. A. Hinde (University of Cambridge) reported on his study of infant-mother separation in rhesus monkeys, and showed that finely controlled intervention can yield precise data which may be swamped in more drastic experiments. It was surprising to learn that it is apparently less traumatic for the (6 month old) rhesus infant to be isolated from the cage group, including its mother, than for the infant to be left with the group after removal of the mother.

Dr J. P. Hess (University of Basle) described a detailed study of the sexual behaviour of the lowland gorilla in Basle Zoo. This study deserves a special note because of the virtual impossibility of observing such behaviour in the wild. Dr Hess backed up his data with a film which illustrated the striking invitation behaviour of captive gorilla females and demonstrated the finer points of mating behaviour.

The session on human ethology attracted particular interest and included an excellent lecture on human sexual dimorphism by Dr Corinne Hutt (University of Reading). After outlining some of the biochemical and physiological evidence for early sexual differentiation in human beings, Dr Hutt summarized her observations on early differences in behavioural development in human infants. The important question of cross-cultural comparison of human behaviour was broached by Dr N. Blurton Jones (University of London), who made a preliminary report on a combined study of Bushman and London children. Many qualitative similarities were seen in this study; but there were also many quantitative

Black Holes against Neutron Stars

Is mass the single vital factor in determining whether a given star will evolve into a neutron star or a black hole? As stellar evolution theory has developed, the importance of the role taken by rotation has become increasingly clear, and it now looks as though this is particularly true at the end point of stellar evolution.

In next Monday's *Nature Physical Science* Sabatino Sofia presents calculations showing just how rotation affects these late stages of a star's life. If the rotational velocity of the star is high, then, as might be expected naively, a large amount of matter is shed during the evolution and the remaining core can settle down as a neutron star. But if the velocity is low, little mass can be lost and the core collapses.

The interesting question, of course, is just where the dividing line comes. According to Sofia, the condition for the

formation of a neutron star turns out to be that the angular momentum of each element satisfies the inequality

$$L > \sqrt{10^6 GM_r}$$

where M_r is the mass interior to the element. But this is still only half of the required solution. Applications to real stars depend on knowing realistic mass and angular momentum distributions. By making the crude assumption that no angular momentum transfer occurs after a star leaves the main sequence, Sofia finds that for a $25 M_\odot$ star an angular velocity of 4×10^{-6} cm s⁻¹ is sufficient for stability, and that a $5 M_\odot$ star is stable for angular velocities above 9.6×10^{-6} cm s⁻¹. These limits are unlikely to be more than two or three times smaller than realistic limits. Only very slowly rotating, massive stars can thus evolve into black holes.

differences. Mr P. K. Smith (University of Sheffield) complemented these studies with a demonstration of the use of penetrating statistical tests (principal component analysis followed by factor analysis), which provide a firm basis for analysing clusters of infant behaviour patterns. He confirmed Dr Hutt's observation that English children, at least, exhibit some highly significant sex differences. On a different tack, Dr A. Kendon (Bronx State Hospital, New York) gave a descriptive account of human greeting gestures, largely based on a film record of a party. This particular talk, however, illustrated the fact that human ethology is still hovering between the anecdotal and analytical levels. Systematic data analysis and presentation are necessary to convince sceptics that complex terminology reflects underlying behavioural mechanisms, rather than the verbal creativity of the observer.

MERCURY

In the Atmosphere

from our Geomagnetism Correspondent

THE recent public attention given to the levels of mercury in, for example, tuna fish and swordfish has led Weiss *et al.* (*Science*, **174**, 692; 1971) to investigate the complementary problem of whether or not the atmospheric content of mercury has increased in recent years and, if so, whether the increase may be attributed to man. On the face of it there is good reason for supposing that man's activities may have produced such an increase. The combustion of fossil fuels, the roasting of ores and the production of chemicals with mercury catalysts are all processes which could in theory lead to a significant rise in the mercury level, although there are also known natural processes which could contribute to such a rise. What Weiss and his colleagues have thus set out to do is to make quantitative estimates of what has been, and is, happening.

Their method has been to determine the mercury content of ice samples ranging in age from 800 BC to the summer of 1965. At the time of their formation ice samples record, and subsequently maintain in essentially unchanged condition, the composition of the atmosphere. Strictly speaking, the composition recorded is the composition of the materials which are washed out from the atmosphere by the relevant precipitation; but because rain effectively removes mercury from the atmosphere it may be confidently assumed that the mercury content of ice may be equated to the corresponding mercury content of the atmosphere. By analysing ancient ice samples and dating them using such methods as ^{210}Pb and fission product geochronology, oxygen isotope

analysis or firm stratigraphy, it is thus possible to estimate the composition of the atmosphere as a function of time depending only on the availability of samples.

In this case the ice samples were taken from Greenland and Antarctica. The results indicate a significantly higher rate of deposition of mercury in recent years. Ice samples formed before 1952 had mercury contents ranging from 30 to 75 ng per kilogram with a mean value of 60 ± 17 . By contrast, the mean value for the period 1952–1965 was 125 ± 52 ng per kilogram with a range of 87–230. The mercury content of the atmosphere has thus apparently increased by an average factor of two since early historic times.

To investigate the cause of this increase Weiss and his colleagues have attempted to calculate the relative contributions of mercury to the atmosphere from both natural and industrial processes. Clearly any such calculations must make many oversimplifying assumptions and the results can thus only be regarded as orders of magnitude; but in the sense that some of the computations may be made in different ways starting from different assumptions there are certain inbuilt checks on the validity of the results.

The flux of mercury from the continents to the atmosphere arising from natural processes is thus calculated by Weiss *et al.* to be in the range 2.5×10^{10} to 1.5×10^{11} per year. By contrast, the flux of mercury from the continents to the oceans by way of rivers is much less—a maximum of 3.8×10^9 per year.

Neither can industrial processes compete with the natural continent-atmosphere transfer, apparently. The mercury lost to the atmosphere in chlor-alkali production is estimated at 3×10^9 g per year; cement manufacture adds another 10^8 g per year; the roasting of sulphide ores could give another 2×10^9 g per year; and Bertine and Goldberg (*Science*, **173**, 233; 1971) recently showed that an upper limit of 1.6×10^9 g of mercury per year can be released to the atmosphere through the burning of coal, oil and lignites.

Why, then, has the mercury content of the atmosphere recently increased by a factor or two? Weiss and his colleagues speculate that man is, in fact, responsible but not in the most obvious way. They attribute the natural transfer of mercury to the atmosphere to the degassing of the Earth's upper mantle and lower crust—a thesis supported by the fact that mercury is enriched in sedimentary compared with igneous rocks and the fact that atmospheric mercury concentration depends on barometric pressure.

INDUSTRIAL HEALTH

Exposure to Asbestos

from a Correspondent

ASBESTOS is an insidious pollutant. But because of its widespread industrial application as an insulator many workers are liable to be exposed to its effects. In a study of workers in a New England shipyard whose job was to cover pipes with an asbestos layer, signs

Role of Initiation Factor F3

IN *Nature New Biology* next week Ochoa and his colleagues, in two reports, describe their latest probings of the function of factor F3, one of the initiation factors responsible for catalysing the association between ribosomes, messenger RNA and the initiating species of aminoacyl-tRNA, fmet-tRNA_f, at the start of protein synthesis. Sabol and Ochoa show that factor F3 is not only required for the binding of messenger RNA to the small 30S ribosomal subunit at the beginning of translation but is also required for the dissociation of 70S ribosomes released from a messenger when they have completed a round of protein synthesis.

Sabol and Ochoa's experiments indicate that 70S ribosomes released from a messenger are dissociated when a molecule of F3 binds to the 30S subunit of the 70S ribosome. The released 30S subunit, with a molecule of F3 still attached, is then available to associate with another messenger molecule to form an initiation complex. Once this

has happened the molecule of F3 is displaced as the 50S ribosomal subunit binds to the complex to form a 70S ribosome capable of completing the translation of the messenger. The liberated molecule of F3 meanwhile is free to dissociate another 70S ribosome running off the end of a messenger and so the cycle continues.

Factor F3 thus plays a crucial part in potentiating the 30S ribosome and Lee Huang and Ochoa report further evidence that different species of F3 factors exist in *Escherichia coli* which can discriminate between different species of messenger RNA and therefore regulate which are translated. They find that two F3 factors purified from *E. coli* infected with phage T4 and from uninfected cells differentially promote the translation of early and late T4 messengers and phage MS2 RNA. One factor promotes translation of MS2 and early T4 messenger RNAs and the other promotes translation of late T4 messengers.

of asbestosis were eleven per cent more common than in controls taken from other shipyard workers.

The disturbing feature of this report is that the pipe coverers were working in an environment where the exposure to asbestos dust was at about the recommended maximum level thought to be safe. This research is described in the *New England Journal of Medicine* by a group from the Harvard School of Public Health and the Boston medical school (285, 1271; 1971), and is an invaluable account of the condition of workers in an asbestos environment that is known from long term studies to have been more or less constant for twenty years.

There is no specific diagnostic test for asbestosis so that the diagnosis depends on the presence of symptoms such as shortness of breath on exercise, X-rays of the lungs, tests of respiratory function and clinical findings, particularly auscultation of the lungs for the character of the breath sounds and the occurrence of abnormal sounds. Other dust-induced lung diseases lead to similar signs and symptoms; the final diagnosis depends on a history of exposure to asbestos.

In the present investigation, the exposure to asbestos was not in doubt. What the investigators wished to discover was the extent to which the workers in an environment thought to be safe showed respiratory disorders attributable to asbestosis. To minimize the subjective elements the X-rays were examined independently by three radiologists, and criteria were established for the diagnosis of asbestosis based on the presence of a number of clinical abnormalities.

The control group was matched for age, duration of employment, height and weight, smoking habits, marital status, and location of residence. The pipe coverers had been employed in the shipyard for an average 17.4 years and the controls 17.1 years.

The striking result of the survey is that of 101 pipe coverers (compared with 94 controls), thirty-eight per cent of workers with twenty years of cumulative exposure had asbestosis.

Although slow in onset—asbestosis was never diagnosed in men with less than ten years' cumulative exposure—asbestosis progresses to a severely disabling and ultimately fatal disease impairing the function of the lung. Small fibres, when inhaled, can penetrate the tissue of the lungs causing reactions which lead to destruction of normal lung tissue. Apart from being itself a lethal disease, asbestosis lowers the resistance to pulmonary tuberculosis and increases the liability to cancer of the lung.

This painstaking survey of the shipyard will no doubt play an important

part in the establishment of threshold limits for exposure to asbestos dust, and as the *New England Journal of Medicine* says in an editorial, the threshold limit value should be lowered far below some recent proposals.

DNA REPLICATION

RNA Primer

from our Cell Biology Correspondent

A LITTLE may be known about the biochemistry of the semi-conservative replication of DNA but, as a glance through the contents tables of the current batch of journals shows, that is not for want of trying. Brutlag, Schekman and Kornberg (senior), for example, report (*Proc. US Nat. Acad. Sci.*, 68, 2826; 1971) an intriguing set of observations which they believe indicates that RNA polymerase is involved in the initiation of replication of single standard, circular M13 DNA; they suggest that the RNA polymerase may act by providing an RNA primer molecule onto the 3' hydroxy group of which DNA polymerase initiates DNA synthesis.

Brutlag *et al.*'s observation is simply that the conversion of single stranded M13 DNA to a double stranded replicative form and the subsequent replication of the replicative form in *Escherichia coli* is blocked by rifampicin, a specific inhibitor of *E. coli* RNA polymerase. Furthermore, as expected from this observation, this block to replication of M13 DNA is not seen when *E. coli* cells, which have an RNA polymerase

mutated to resistance to rifampicin, are infected in the presence of the drug.

Not so long ago the suggestion that an RNA chain might prime DNA polymerization would certainly have been viewed askance, but now that Baltimore's group (Verma *et al.*, *Nature New Biology*, 233, 131; 1971) have shown that reverse transcriptase initiates DNA synthesis, directed by an RNA template, on an RNA primer such a suggestion is unlikely to cause any great stir. Indeed, Verma *et al.* themselves suggested that DNA polymerases like reverse transcriptase might initiate DNA synthesis with an RNA primer.

In the same issue of the *Proceedings* (*ibid.*, 2839) Inselburg and Fuke report that minicells produced by the mutant strain of *E. coli*, P678-54, which carries the colicin E1 genome, contain colicin E1 DNA but no cellular DNA. The circular colicin E1 genomes in these minicells seem to continue to replicate and various catenated and replicating E1 DNA molecules can be extracted. According to Inselburg and Fuke the behaviour of these colicin DNA molecules when sedimented in sucrose and caesium chloride-ethidium bromide density gradients indicates that both Cairns-type double forked circular molecules and Rolling circle-type circular molecules with linear tails are present.

Elsewhere, Strätling and Knippers (*J. Mol. Biol.*, 61, 471; 1971) relate their latest observations of DNA synthesized by DNA-membrane complexes isolated from *polA*⁻ mutant *E. coli* cells. These cells lack DNA polymerase I (Kornberg enzyme) activity but have at least one

Location of Calcium Ions in Striated Muscle

STUDIES on the structure of muscle filaments have gradually made clear a general framework for hypotheses on the mechanism of muscle contraction. The basic force-developing step is still elusive, however, and there are also several features about the "switching on" process about which very little is certain. It is useful therefore to have any new information on these events, and a report by Yarom and Meiri of the Hebrew University, Jerusalem, in next Wednesday's *Nature New Biology* describes some experiments designed to fix the location of the chief storage site for calcium ions.

Potassium pyroantimonate has previously been shown to precipitate calcium in cardiac muscle, and Yarom and Meiri used this method to precipitate and thus locate the calcium ions in striated muscle. The muscle was treated with a solution of sucrose, potassium pyroantimonate and the fixative osmium tetroxide at pH 7.2. Electron micro-

graphs of longitudinal sections of these muscles showed stain between the myofilaments and it concentrated in particular along a line in the I band known as the N₂ line. The two N lines are densely staining lines in the I band and the N₂ line differs from the N₁ in that the distance of the N₂ line from the Z lines increases with sarcomere length. The muscles were then tetanized electrically through the nerve and fixed during the tetanus plateau. Longitudinal sections from such muscles did not show predominantly stained N₂ lines, but the stain was dispersed along the myofilaments. Additional muscles were treated with EGTA, a strong calcium chelating agent, and were then treated with pyroantimonate and the osmium tetroxide fixative. No myofibrillar deposits were observed in longitudinal sections of these muscles.

Thus, Yarom and Meiri suggest, it is possible that the N₂ lines are sites for the storage of intracellular calcium.

other residual DNA polymerase activity, DNA polymerase II, which can be isolated free of membrane and template. The DNA-membrane complex obtained from these cells continues for short periods to synthesize DNA *in vitro* (whether this synthesis is brought about by DNA polymerase II is an open question). The DNA made *in vitro* sediments with the bulk template parental DNA until the protein component of the complex is removed. After the removal of the protein the DNA made *in vitro* sediments as fragments ranging in sedimentation coefficient from 10S to 25S. At least some of these fragments, the 10S fraction in particular, seem to contain molecules in which parental and DNA sequences made *in vitro* are covalently linked while the remainder of the fragments seem to comprise parental DNA hydrogen bonded to DNA made *in vitro*. Moreover, kinetic studies indicate that the covalent linkage of parental and *in vitro* DNA chains is transient.

Strätling and Knippers believe that these observations indicate that parental DNA is nicked by endonucleases to produce free 3' hydroxy termini which not only allow free rotation of the DNA strand but also serve as a primer for DNA synthesis. They further suggest that the parental/progeny molecules so produced are cut by endonucleases to separate parental from newly made DNA and then the two sorts of DNA fragments must be relinked to form continuous parental and progeny strands.

Strätling and Knipper's data, as they comment, are consistent with Haskell and Davern's model which envisages that DNA replication involves the introduction of nicks ahead of the replication fork, with the nicked pieces serving as primers for DNA synthesis. The recent experiments of Werner (*Nature*, **230**, 570; 1971) also indicate that progeny and parental DNA chains are transiently linked by covalent bonds, although Werner interprets his findings differently. In short, it seems that during *E. coli* DNA synthesis parental and progeny sequences are linked but how and why remains to be unequivocally explained.

HAEMOGLOBIN

Models for All Tastes

from our Molecular Biology Correspondent
AS to the choice of a kinetic scheme for haemoglobin oxygenation, most workers in the field will still prefer, like H. L. Mencken's politician, to sit on the fence while keeping both ears to the ground. Although the structural differences between the oxygenated and deoxygenated states have been defined in minute detail

by Perutz, who was able to infer from them many features of the mechanism of oxygenation, this has been insufficient to quell the wrangle about which of the several feasible mechanistic models best fits the equilibrium and kinetic data.

MacQuarrie and Gibson (*J. Biol. Chem.*, **246**, 5832; 1971) have gathered some interesting evidence from a comparison of carbon monoxide binding rates and release of the cofactor, 2,3-diphosphoglycerate, which binds in a ratio of one molecule per haemoglobin tetramer to the deoxygenated form only. More exactly, they have used a fluorescent analogue of diphosphoglycerate, a hydroxypyrenetrisulphonate, which competes with the cofactor for the single site, and has a qualitatively identical effect on the oxygen uptake curve. The binding of this form is easily measured, for when it is bound its fluorescence is quenched by the haem groups.

When carbon monoxide is introduced into a solution of haemoglobin containing some of the cofactor, the kinetics of binding of ligand and release of cofactor

can be simultaneously measured by fast spectroscopy. It is at once apparent that the two processes follow different rates. This leads immediately to the conclusion that intermediate oxygenation states occur in significant concentration. MacQuarrie and Gibson then go on to interpret their results in terms of alternative ligand binding mechanisms, assuming only that there are not more than two affinity states in respect of the cofactor. They fit the rate data first in terms of an Adair model, with four sequential binding reactions, in which the liganded conformational state reacts rapidly with carbon monoxide and does not bind the cofactor. The cofactor, in this scheme, is released after the attachment of the third haem ligand. A least-squares fit of both the carbon monoxide and cofactor binding curves shows that this formation is capable of satisfying the observations within the error of the experiment. If, on the contrary, one assumes that the cofactor is released after binding the second ligand, the fit is much worse (though one

The Lymphocyte Trap Sprung

THE jargon of the cellular immunologist contains words such as population, microenvironment, migratory, which would be perfectly proper on the lips of an ecologist. This perhaps provides a clue to some of the present trends in cellular immunology because to an ever increasing extent lymphocytes are being studied in relation to their environment. It is quite feasible to think of lymphocytes as organisms of which the behavioural, morphological and functional characteristics can be arranged in relation to their environment in the intact vertebrate. Such a concept stresses that the lymphocyte in its most interesting form is abundantly alive. The old days of the strictly morphological approach based exclusively on the perusal of long dead slices of tissue are happily past.

In *Nature New Biology* next Wednesday (December 22), Zatz and Lance present a communication entitled "Lymphocyte Trapping in Tolerant Mice". This study, with its undertones of polecats and the frozen North, concerns the phenomenon of retention of migratory lymphocytes in lymphoid organs which are involved in responding to an antigenic stimulus. The method is simple. Lymphocytes are labelled with ⁵¹Cr *in vitro* by incubation in an appropriate solution of "hot" sodium chromate. Subsequently, the labelled cells are injected intravenously into mice at various times after antigenic stimuli. It is a reasonable approximation to say that for a day or so the amount of radioactivity found in various lymphoid

organs of the body will be an accurate indicator of the presence of the labelled cells. The lymphoid organs are always harvested 24 h after the injection of labelled cells.

Lance and his associates have previously demonstrated that in lymph nodes which drain the site of application of a foreign skin homograft more of the injected cells were found than in comparable nodes which drain the site of a skin autograft. The maximum differential between the two kinds of node was observed at about the tenth day after application of the skin homograft, before the graft itself is rejected. The functional significance of the phenomenon cannot at the moment be specified but in their most recent experiments Zatz and Lance find that in parental mice rendered tolerant by neonatal injection of F₁ spleen cells trapping does not operate in the lymph nodes draining the site of an applied (and tolerated) skin homograft.

In other studies it has been shown that some degree of engorgement of lymph nodes can follow the introduction into afferent lymphatics of some of the products of stimulated lymphocytes (Kelly, R. H., *Clin. Exp. Immunol.*, in the press, 1972). It is tempting to suppose that some such mechanism is operating (or failing) in the lymph nodes of the mice of Zatz and Lance. It will be interesting to learn when and with what intensity the trap operates in animals which have been injected with either immune or normal cells in order to break the tolerant state.

is throughout concerned only with deviations of up to a few per cent at worst, because three variables are available for fitting, and the calculation is insensitive to the last binding step).

For the all-or-none, allosteric, model of Monod, Wyman and Changeux, using for the three adjustable parameters the equilibrium constant relating the high and low affinity states of the protein, the ratio of their ligand affinities and one of the two rate constants demanded by the model, the fit is again poor. It may be noted that the release of diphosphoglycerate after oxygenation of the third haem was earlier deduced by Tyuma *et al.* (*Biochem. Biophys. Res. Commun.*, **43**, 423; 1971), simply from a comparison of the parameters defining the oxygen dissociation profiles in terms of the Adair equation, in the presence and absence of the cofactor. They were able to show moreover that the last oxygenation step could be quantitatively identified with the reaction of an isolated β -chain.

These results then are without doubt strong arguments in favour of one type of model. At the same time, Hopfield *et al.* (*J. Mol. Biol.*, **61**, 425; 1971) have been at pains to show that assorted rate data garnered from the literature are at no point inconsistent with an allosteric formulation. The oxygen saturation rate curves are adequately fitted in such terms, though not as well as by a set of Adair constants. Hopfield *et al.* regard such curve fitting as suspect, however, and insufficient evidence in favour of a model. Their own preference is based essentially on the ability of the allosteric formalism to absorb published data on the changes in concentration of rapidly reacting haemoglobin with the extent of ligand dissociation caused by flash photolysis.

At a more utilitarian level, and as a postscript to my account recently of the use of cyanate and related compounds to inhibit the sickling reaction in sickle cell anaemia, there is a new study by Gillette, Manning and Cerami (*Proc. US Nat. Acad. Sci.*, **68**, 2791; 1971). These workers, who were responsible for the original (and successful) attempt to mitigate sickling by reacting the chain termini of the abnormal haemoglobin with cyanate, have now examined the effect of such modification on the survival of the red cells in the patient. Cells, labelled with isotopic chromium, were treated with cyanate and then returned to their owner. The half-population survival time increased from an average of 10 to 21 days, which compares much more favourably with the 20–35 days survival span of normal cells. The latter were essentially unaffected by cyanate ion. This result then may turn out to be one of the occasional triumphs of the biochemist over a baleful phenomenon of nature.

Ribonuclease and Reverse Transcriptase

FEW molecular biologists today would quarrel with the idea that infection of cells by RNA tumour viruses depends on the synthesis of a double stranded DNA molecule, the provirus, specified by the single stranded RNA genome, and that this synthesis is catalysed by reverse transcriptase. Baltimore and his colleagues have shown (*Nature New Biology*, **233**, 131; 1971) that reverse transcriptase is similar to DNA polymerase I of *Escherichia coli* and requires a primer with a 3' hydroxyl group on which to initiate DNA synthesis, and countless groups have by now shown that an RNA/DNA hybrid molecule and some single stranded DNA molecules are intermediary to the appearance of double stranded DNA. Mölling and five colleagues working in Tübingen now report in next Wednesday's *Nature New Biology* the discovery of a ribonuclease activity, RNAase H, which seems to be responsible for the displacement of single stranded DNA from RNA/DNA hybrids.

Having recently isolated, from calf thymus cells, and RNAase which specifically digests the RNA strand of RNA/DNA hybrids, Mölling and his associates searched for a similar sort of activity in avian myeloblastosis virus particles

(AMV) and sure enough they found it. Preparations of AMV particles disrupted with detergent will digest the RNA of RNA/DNA hybrids made either by transcribing calf thymus DNA with *E. coli* RNA polymerase or by annealing phage fd DNA with complementary RNA.

Mölling *et al.* then attempted to fractionate this RNAase H activity from the AMV virions but none of the several separation methods they used resulted in the separation of reverse transcriptase activity from RNAase H activity. Indeed the degradation of the single stranded RNA in the AMV particles by endogenous RNAase H was found to depend, at least in part, on the reverse transcription of this RNA. This discovery suggests that RNAase H activity is responsible for generating single stranded DNA during the synthesis of a provirus and it may well be that the polymerase and the ribonuclease activities reside in the same enzyme molecule. There is, of course, a precedent for this situation. DNA polymerase I of *E. coli* has both DNA polymerase and DNAase activities; the already considerable parallels between reverse transcriptase and DNA polymerase I may, therefore, extend still further.

Surface Characteristics of B Cells

CELLULAR immunologists are now devoting much effort to describing the heterogeneity of lymphocytes which, to the despair of the old-fashioned morphologist, look exactly alike. The efforts are directed partly to arrive at satisfactory counts of say B or T cells in various species, particularly man and, partly, to determine the functional attributes of lymphocytes. In next Wednesday's *Nature New Biology* two groups of immunologists, Fröland, Natvig and Bernal, and Dwyer, Mason, Warner and Mackay, report work which reflects these aims.

Fröland *et al.* have approached the problem of identifying B cells in man by the use of fluorescent anti-immunoglobulin antisera. Most theorists suppose that the capacity of B cells to be stimulated to antibody production depends initially on their possession of antibody-like receptors on the cell surface. Using a battery of more or less specific antisera conjugated with a fluorochrome marker, Fröland *et al.* found that up to 10 per cent of the peripheral blood lymphocytes from six normal patients showed visible fluorescence indicative of surface bound immunoglobulin. The monospecific antisera which were class or sub-class specific reacted with smaller percentages of cells. The marginal indication

was that different cells carried different immunoglobulins on their surfaces. In contrast the blood lymphocytes from six patients with Bruton type agammaglobulinaemia, a complaint associated with failure to produce serum antibody, showed no staining with any antisera.

Wilson and Nossal using another technique (*Lancet*, ii, 788; 1971) have recently arrived at a figure of 34 per cent for the frequency of human lymphocytes with a high density of surface-bound immunoglobulin. The discrepancy between these results and those of Fröland *et al.* is probably indicative of a difference in sensitivity of the two techniques. But it is clear that with either method the surface-bound immunoglobulins are probably a sound characteristic of human B cells.

Dwyer *et al.* incubated spleen cells from nude mice, which are widely believed to be congenitally athymic, with a variety of different radioactively labelled antigens. They find that the proportions of labelled cells ($3-18 \times 10^{-4}$) were not significantly different between nude and normal mouse spleen cells, suggesting that only B cells are antigen binding cells (ABC as they say). In a sense this work dovetails nicely with the previous studies on immunoglobulins on the surfaces of B cells.

Roderick Murchison, Geologist and Promoter of Science

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Sir Roderick Impey Murchison (1792—1871) was a great stratigrapher who also made an impact on the British Association, the Geological Survey and the Royal Geographical Society.

SIR RODERICK MURCHISON died on October 22, 1871. He had taken up the study of geology as an amateur in 1824, largely by chance, at a time when the science was young and fashionable, and opportunities to attain distinction were wide open to any reasonably intelligent enthusiast who was fond of an open air life. This was particularly so for those who possessed sufficient private means to permit the devotion of their whole time to the subject, and this Murchison was able to do.

Roderick Murchison came from a west Highland family. He was the elder son of a doctor, Kenneth Murchison, who retired to a small estate at Tarradale in Easter Ross in the north of Scotland after making a fortune in India. Roderick Murchison was born here on February 19, 1792. He was educated at Durham Grammar School, and then entered the military school at Great Marlow. At the age of fifteen he received a commission in the 36th Regiment, and a year later saw active service in the Peninsular War, and was with Sir John Moore in the retreat to Corunna. After the defeat of Napoleon at Waterloo in 1815 it seemed to Murchison that prospects for further advancement in the army were small, and he retired with the rank of captain. He then married a lady of cultivated taste, and with her spent two years, chiefly in Italy, studying art and antiquities. At this time he acquired the habit of taking careful notes of all he saw, a practice that was to stand him in good stead later on in his geological work.

Murchison returned to England in 1818 and sold the family estate which he had inherited. He then settled, first in the north of England, and later at Melton Mowbray in Leicestershire. For the next few years he lived the life of a country gentleman, becoming one of the best known fox hunters in the Midlands.

A chance meeting with Sir Humphry Davy in 1823, at a partridge shoot, changed the whole course of Murchison's career. Davy suggested that he should take an interest in science and promised that he would soon get him into the Royal Society. The thought of giving up field sports would not have appealed to Murchison, but he concluded that if so distinguished a scientist as Davy could find time to indulge in them, then so could he; and so, encouraged by his wife, an amateur naturalist, he moved to London in 1824.

After arrival in London, on Davy's advice he attended W. T. Brande's lectures on chemistry and geology at the Royal Institution. He found that geology appealed to him particularly, so he began to study the subject seriously and became a member of the Geological Society of London. Soon he attracted the attention of some of the more prominent members of the Geological Society, notably William Buckland and Adam Sedgwick. In fact he seems to have very quickly impressed his personality not only on the members of this society, but on intellectual and social circles generally in London. Davy kept his promise, and in 1826 Murchison was elected a Fellow of the Royal Society not, obviously, on account of his scientific work,

but because he was an independent gentleman having a taste for science, with plenty of time and money to gratify it. Such was the custom at that time.

Murchison was no dilettante, however, for he worked hard to make himself proficient in his new occupation, pursuing the study of geology with all the energy and enthusiasm he had formerly expended in the hunting field. He was fond of social activities, and these, no doubt, helped him in his career.

He soon became involved in the affairs of other organizations. In 1830 he became a founder member of the Royal Geographical Society and he was one of the earliest and most active promoters of the British Association for the Advancement of Science, which met for the first time in York in 1831. He took an active part in the affairs of both these societies for many years, but geology for long remained his principal interest. He was appointed a secretary of the Geological Society in 1826, elected president in 1831, and served on its council until almost the end of his life. For some thirty years after joining the society he devoted much of his life to geological field work. He travelled extensively in the summer months, both in Britain and over much of Europe, carrying out geological research and widening his knowledge. During these tours it was his habit to make the acquaintance of local geologists and absorb all the information he could from them.

One of his earliest journeys took him in 1826 to Brora in Sutherland, to examine its isolated coalfield, the age of which was at that time disputed. After a stop at York, he spent two days with the veteran English geologist William Smith, studying the Jurassic rocks of the Yorkshire coast. The information he gained from Smith helped him to establish the Jurassic age of the Brora coalfield, but he probably benefited even more from Smith's long experience of stratigraphical palaeontology. At all events, the two got on well together, and later on Murchison was one of those who supported an application to obtain a Civil List pension for Smith.

Stratigraphy

Stratigraphy was the branch of geology that appealed most to Murchison and it was as a stratigrapher that he made his name. About 1830 there was still one important gap in contemporary knowledge of the rock succession in Britain. Very little was known about the Lower Palaeozoic sediments below the Old Red Sandstone, apart from the facts that they occupied considerable areas and that they included some fossiliferous beds. They were called either "transition" beds, the name given to them by A. G. Werner, or simply "greywacke slates". Murchison's friend Sedgwick had started studying them in the Lake District and North Wales, but there was scope for investigation elsewhere. Murchison, on Buckland's advice, decided to examine the outcrops of these rocks in South Wales and the Welsh borderland.

Early in 1831 he set out, accompanied by "his wife and maid, two good grey nags and a little carriage, saddles being strapped behind for occasional equestrian use". This was the start of an investigation that lasted for several years. It resulted in the establishment, on the basis of fossil evidence, of an entirely new geological system, the Silurian System (much later to be divided into two systems, the Silurian and the Ordovician). The results were published in 1839 in Murchison's most famous book, *The Silurian System*, which was accompanied by a large

geological map covering a large part of Wales and the adjoining parts of England. This was a major achievement, not only as far as British geology was concerned but for geology as a whole, for the Silurian system was soon adopted by geologists throughout Europe and in America.

Murchison had been fortunate in undertaking the investigation of a series of rocks so little known. He extended his investigation of these rocks farther afield. It had come to his notice that in north-western Europe, particularly in Russia, there were vast areas of sedimentary rocks, undisturbed by Earth movements, which contained fossils similar to those found in the Silurian rocks in Britain. Murchison quickly seized the opportunity they offered, and in the summer of 1840 he set off for Russia to investigate them. He was accompanied by a French geologist, E. de Verneuil, a skilled palaeontologist. The journey, which lasted about three months, included regions in the neighbourhood of St Petersburg (Leningrad) and Moscow, and extended as far north as Archangel. This expedition was something of a preliminary canter, for Murchison was to visit Russia again; and canter is perhaps the right word, for he has described how the party rushed through the country in an open carriage drawn by five or six horses at a speed of ten to twelve miles an hour. Much of the country was in fact a flat drift covered plain in which exposures were few. Murchison, however, had the faculty of recognizing the salient geological features of a country quickly. During their tour the travellers proved the presence in northern Russia of a complete succession from the Silurian up to the Carboniferous, but Murchison brought back information of more immediate importance.

He and his companion had found beds containing fishes of Old Red Sandstone type interbedded with sediments containing marine fossils. This resolved beyond doubt a controversy in which he and other well-known British geologists had been engaged a few years earlier, the question of whether certain rocks in Devonshire containing marine fossils were coeval with sediments of Lower Old Red Sandstone age found in other parts of Britain. This discovery led to the establishment of another new geological system, the Devonian, the sandstones of the Lower Old Red Sandstone forming a continental facies of the system. Murchison was largely responsible for the establishment of this system.

Return to Russia

Murchison returned to Russia at the end of April 1841, again with de Verneuil, and this time a Russian geologist, Count A. von Keyserling, accompanied them. Through the British ambassador, Murchison made contact with Russian officials, and discussed his project with the Emperor of Russia. This was fortunate, for the expedition was greatly facilitated by official help and hospitality wherever it went; guides were particularly necessary, for detailed topographical maps were seldom available.

The area examined was extensive, including central and southern Russia and the Ural mountains. During this expedition the travellers outlined the stratigraphy and determined the broad general structure of the rocks in this area; they effected a general correlation with the sediments of western Europe.

Soon after his return Murchison announced that he had established, on stratigraphical and palaeontological evidence, yet another geological system overlying the Carboniferous and older than the Jurassic. This was the Permian, named after the Russian province in which it was best developed. It was soon realized that sediments well known in Germany, and also the Magnesian Limestone in the north of England, fitted into this system. The results of this Russian expedition were published by Murchison, de Verneuil and von Keyserling in 1845 in *The Geology of Russia in Europe and the Ural Mountains*. In 1856 Murchison, in collaboration with the Scottish geologist James Nicol, published a large geological map of Europe, on which the Silurian, Devonian and Permian rocks were differentiated.

Murchison had by now established for himself a European reputation, particularly for his work on the Palaeozoic rocks.

His field work had not been confined to the Palaeozoic, however, for he had published important papers on other stratigraphic formations, and he continued to publish on British and continental geology for the next ten years. In 1854 his well-known book, *Siluria*, appeared, containing a wide ranging summary of all that was known about Silurian rocks at the time and discussions of cognate subjects. The fourth and last edition was published in 1867.

Geological Survey

In 1855 Murchison, the amateur, in effect turned professional. In his sixty-fourth year he was appointed to succeed Sir Henry de la Beche as Director-General of the Geological Survey and Museum, and of the Metropolitan School of Science applied to the Arts. The circumstances leading to this appointment were unusual. Concern had been expressed by members of the Geological Survey that a "most estimable man of a good family but possessing only a very slender acquaintance with geology" was likely to be appointed. As a result of a petition by eminent geologists outside the Survey the appointment was offered to Murchison. Changes were in the air, and it was planned (with the backing of the Prince Consort) to establish a great teaching establishment for science and technology at South Kensington. There was a possibility that the survey might lose its independence, and it was therefore a distinct advantage for it to have so influential a director. The appointment was a success, and he held it until his death some sixteen years later. One of his successors as director has said that "his eminence as a scientific man, his social position and wealth, his personal friendship with eminent politicians and members of the aristocracy, and his genial, forceful, assertive individuality made him an eminently successful director".

As a geologist, Murchison had his successes, but he also had his limitations, and he made mistakes. He was a keen-eyed and careful observer, with the power of marshalling facts, and he was a very hard worker. He lacked imagination, however, and his mind was not of the sort that evolves broad principles and new laws, but he was shrewd enough to know his own limitations and where his strength lay. His greatest success was as a stratigrapher, and in this field his work was of outstanding importance. On the other hand he was a strong opponent of the glacial theory introduced into this country in 1840 (though he was not alone in this); and he was sceptical of some of the new ideas about physical geology adopted during his lifetime. He refused to accept that the geological record lent any support to Darwin's theory, and Darwin, in a letter to Sir Charles Lyell, remarked: "How singular so great a geologist should have so unphilosophical a mind". Nor would he accept that the work of his old friend Adam Sedgwick on the Cambrian rocks established them as a separate geological system, and in his publications they were always treated as Lower Silurian. This disagreement led eventually to the estrangement of the two geologists.

Geologist and Geographer

Murchison's activities as a geologist had not prevented him from taking a prominent part in the affairs of the Royal Geographical Society, and during his later years he was probably more widely known for his connexion with this society than as a geologist. Though not a geographer in the modern sense, he had travelled widely, and he was very much in sympathy with the principal function of the society in the nineteenth century, the promotion of exploration in all parts of the world. In fact, his name has been perpetuated around the world in the naming of more than a dozen rivers, mountain ranges and so on. He served as president of the Royal Geographical Society for no less than seventeen annual terms, his final term of office extending from 1862 until his death. Features of the years in which he served as president were his anniversary addresses, which averaged 30,000 words in length and were all compiled by Murchison himself (though using

contributions from other hands). They were delivered in abstract, but printed in full; and they provide a comprehensive review of the progress of geographical science and exploration during the first forty years of the society's existence. Apart from his public duties as president, Murchison did much behind the scenes to promote the affairs of the society. He was also largely responsible for the establishment of a separate section, E, for geography at the meetings of the British Association, and was first president of the section, at Ipswich in 1851.

Murchison had, in fact, taken a prominent part in the affairs of the British Association from its inception, particularly during the first ten or fifteen years of its existence, when not all scientists were in favour of its activities, and it was often ridiculed, especially by *The Times*. Murchison was president at the Southampton meeting in 1846. Referring to articles in *The Times* that year he protested against their "ribald vulgarity and ignorance", saying that he was ashamed that his "eminent foreign friends should go away with the impression that *The Times* in its vituperation of science represented my country". Murchison was a trustee of the British Association from 1832 to 1870 and a general secretary from 1836 to 1845.

He seems to have played a less prominent part in the affairs of the Royal Society, though he was one of those who opposed the election of the Duke of Sussex as president in 1830, on the grounds that a scientific man was preferable. The duke was elected by a small majority, and being a wise man, chose to select his council from those who had opposed him, for they chiefly represented science in the society. Murchison, being among those chosen, "deemed it his duty to accept office under a prince who could act so liberally and kindly towards his opponents". He received the society's Copley Medal in 1849

for his services to geological science, in particular for his work in establishing the Silurian System.

As a promoter of science there is no doubt that Murchison played an effective part. He worked very hard, for many years, on behalf of the several societies to which he belonged; and possibly of equal value were his activities in publicizing science, through the British Association and by other means. He and his wife held prominent positions in London society, and his wealth permitted him to entertain lavishly. The receptions held at his house in Belgrave Square were attended by both scientists and prominent politicians. Thus, Murchison was able to exercise very considerable influence in official circles whenever he thought it desirable to do so in the interest of science as a whole, or even of individual scientists. His considerable wealth also enabled him to support and encourage the advance of science. Just before he died he persuaded the government to found a chair in geology in Edinburgh University, and contributed £6,000 towards its endowment. Previously geology had been taught by the professors of natural history, and the Murchison chair in geology was the first separate chair in the subject in any Scottish university. In his will Murchison left £1,000 each to the Geological Society and the Royal Geographical Society, for the promotion of geology and geography respectively, and his name is perpetuated by the annual award of a Murchison Medal by the former society. He is also known to have exercised his influence in all manner of ways to help on individuals in lowly walks of life, particularly if they were interested in science.

Although Murchison had his failings, they were far outweighed by his achievements. He was, in his time, one of the great leaders of science, and his personality gained for scientists as a class greater recognition and respect from society at large.

The Bacterial Cell Surface

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This article deals with some of the foci of activity and current problems in the complex and multidisciplinary field of bacterial cell surface studies.

IN 1965 Bayer and Anderson¹ published an artistic reproduction of what they could see on the surface of negatively stained *E. coli*. In 1971 the secrets of the "mountains" and "craters" of that lunar landscape are still very much with us and hold fascination for an increasing number of scientists. Thin sections or freeze fractured images of bacteria allow one to make out the multilayered three dimensional structure of the bacterial surface²⁻⁴. As a result of careful comparative work with the methods of cytology and biochemistry it is now possible to assign at least a rough chemical composition and biological function to these surface layers^{5,6}. The innermost trilaminar structure adhering to the cytoplasm is the plasma membrane. It contains most of the cellular lipids, as well as protein and carbohydrate, and it forms the main permeability barrier of the cell. It is this structure that is most comparable with the plasma membrane of eukaryotic cells. In some rare instances, in bacteria living in unusual habitats, such as some halophylic bacteria or bacterial L-forms⁷, the plasma membrane is the only surface layer of the cells. In the great majority of bacteria, however, there are several additional surface layers exterior to the plasma membrane. The first one of these is a layer of vary-

ing thickness made up mainly of an extensive network of glycopeptide units: the bacterial peptidoglycan. In spite of some species to species variability in chemical composition, the basic structure of these glycopeptides is remarkably similar throughout the bacterial world: glycan strands made up of a polymer of a disaccharide and an attached network of cross-linked peptides. This bacterial surface component seems responsible for the defined shape and mechanical stability of the cells and most of the effective antibacterial agents as well as viruses cause disintegration of bacterial cells by damaging the peptidoglycan (through inhibition of a biosynthetic step or through enzymic dissolution). Glycopeptides and glycoproteins are, of course, ubiquitous throughout the living world, but the bacterial glycopeptide is unique in its size and shape: it covers the entire surface of the bacterium by what seems to be a continuous, covalently interlinked network of glycopeptide units which on isolation and purification still retain the characteristic shape of the particular bacterium^{8,9}.

In Gram positive bacteria, attached to the peptidoglycan and probably on the outer surface of it, one can find a variety of complex polysaccharides, polyolphosphates or "teichoic acids". These are major antigenic components and can also form the receptors for several bacteriophages. In Gram negative bacteria on the exterior of a thin peptidoglycan layer one can see another trilaminar structure, indistinguishable in dimensions from the plasma membrane. This is the "outer membrane", containing lipopolysaccharide (LPS), lipid and protein material. The great variety of *E. coli* and *Salmonella* serotypes reflect the chemical variability of this LPS struc-

ture^{10,11}. Bacteria with deficient LPS are non-virulent in their vertebrate hosts and therefore it seems that in the absence of homologous antibody the LPS serve as a protective coating against destruction by host phagocytes and serum. Of course, once encountered by the vertebrate host, the protection offered by the particular LPS is annulled by the production of specific antibodies. The immunochemistry of LPS structure is a fascinating record of a continuing evolutionary "chess game" between the bacterium and its vertebrate host: every mutational twist and change in the molecular structure of LPS is matched and counteracted by the production of appropriate antibodies. The outer membrane also contains receptors for specific extracellular macromolecules (for example, colicines) and viruses.

Very little is known about the architectural principles, that is, the bonds (covalent, ionic or others) which hold the various macromolecular units of a single surface layer together, and even less is known about how the various surface layers are anchored to one another and to the cell. A very interesting protein which seems to perform the role of such a structural anchor has been described recently. It forms covalent bridges between the ϵ -amino group of lysine residues in the peptidoglycan and some lipoprotein component of the outer membrane¹².

Specialized Areas of the Surface

In addition to its heterogeneity in depth the bacterial surface also shows distinct horizontal differentiation. Electron microscopic studies of *E. coli* have shown that several hundred points of adhesion between the plasma membrane and the outer layer persist even during extensive plasmolysis. The functional importance of these areas was made clear by the observation that in live bacteria they represent the exclusive areas of attachment for a number of phages, such as T2, T4, T6, ϕ X174 and λ ¹³. It should be remembered that several of these viruses have distinct receptor sites. This finding indicates that clusters of different virus receptors are organized into several hundred distinct topographic areas of the surface.

In order to understand how the combination of binding proteins with their substrates leads to the oriented chemotactic¹⁴ movement of flagella (and the whole cell) it is necessary to understand their fine structure, their mode of insertion into the surface and their spatial relationship to the binding proteins. Progress in such a work was described recently¹⁵.

"Periplasmic" enzymes have now been localized at the cellular tips¹⁶. In *E. coli* a number of specific enzymes (mostly hydrolytic) and binding proteins (implied in chemotaxis and transport) can be released in controlled quantities from *E. coli* by an osmotic shock procedure, in the absence of cell death and without release of a large number of typical intramembrane components.

In many bacteria there is a complete reorientation of surface growth at the site of cell division in the form of septa which move inward to divide the bacterium into two daughter cells of the same genetic and chemical composition, size and shape¹⁷. The cellular control of both the site of initiation and the rate of growth of septa is a central problem in cell division. Biochemical analysis of this problem is just beginning now, following the isolation of a wide variety of genetic mutants and physiological variants in which various abnormalities of septum formation can be observed¹⁸⁻²³.

In streptococci the first observable sign of cell division is the appearance of a local thickening or "notch" in the cell wall at the cellular equator. Next, one can observe the splitting of the notch into two halves, which proceed to move, one to the left, the other to the right of the equator, while the septum grows inward. By the time compartmentalization of the cell is complete the two notches will have reached the exact midpoint between the tips of the parent cell and the completed septum, that is, they are aligned at the sites of the next cell division. Independent evidence indicates that this bilateral movement of cell wall is propelled by the incorporation of

new surface elements at or inside the septum while the "old" hemispheres of the surface are conserved and moved to the left and to the right. These findings reveal an asymmetry of the cell surface: half of the surface (including the original tips of the parent) is one generation older than the other half (which includes the area proximal to the septum of the parent) and the cell wall notches mark the boundary between the two²⁴.

Towards a Functional Anatomy

Not only do the surface lamellae serve as structural components (the only ones that a bacterium has) but built into these layers are the molecular units which determine the specificity of interaction between the bacterium and the thousands of molecules bombarding it from the environment. Whether or not a molecule would be absorbed and transported inside the cell boundaries, or a substance recognized as a chemotactic stimulant, depends on the presence of specific proteins on the surface. The "gates" for the entry of transforming DNA molecules, sites for contact with a virus, a colicine molecule, a hostile *Bdellovibrio* or a friendly bacterium of opposite sexual polarity, survival or destruction by vertebrate macrophages—in short, the entire "social" life of bacteria—depend on the cellular surface.

Which molecular elements of the surface mosaic are responsible for these ectobiological functions? One of the main current activities of the field is to find answers to this question. This involves localization of the various biological activities to the various surface layers as well as attempts to characterize functional units biochemically. It is now becoming possible to solubilize selectively the surface layers into anatomically relevant fractions, that is, into components that correspond to elements recognizable by electron microscopy²⁵⁻²⁸.

Well over sixty specific proteins have so far been localized in the plasma membrane. This includes transport carriers: membrane vesicles prepared from a number of bacteria can carry out energy-driven, specific intravesicle transport of as many as twenty substrate molecules²⁹. Proteins of the electron transport chain, the phosphotransferase II enzymes³⁰, and enzymes catalysing the biosynthesis of membrane lipids³¹, peptidoglycan^{32,33}, teichoic acid^{34,35} and lipopolysaccharide (M. J. Osborn, personal communication) are all localized in the plasma membrane. Many of these enzymes have peculiar physical properties, which distinguish them from cytoplasmic enzymes. Some require lipid cofactors, others are soluble in aqueous solvents only in the presence of detergents. The *C₅₅* isoprenoid alcohol phosphokinase of *Staphylococcus* is completely insoluble in hydrophilic solvents, but can be extracted into butanol. This enzyme purified to homogeneity shows an unusually high content (58%) of nonpolar amino-acids (highest of all proteins as yet isolated³⁶).

The narrow host range of complex biological agents, such as bacteriophages, colicines (extracellular inhibitory macromolecules) or competence factors (agents inducing the ability to absorb DNA from the environment), is based on the presence of surface receptors in the sensitive cells. The solubilization of such receptors has been reported in several instances. Once detached from the bacterium, the recognition of such activities is usually based on a neutralization assay: inactivation of the virus or colicine and so on by soluble fractions prepared from the sensitive (but not from the resistant) bacteria. Fractionation of colicine K receptor³⁷ and solubilization of colicine E3 receptor were reported³⁸. The two activities are distinct and both are located in the outer membrane of *E. coli*. In bacteriophage T4 the lipopolysaccharide receptor seems to react with the part of the tail fibres containing antigens B and C³⁹. Protein-like receptors for two competence factors were localized in the plasma membrane^{40,41}.

The making of the structural heteropolysaccharides of bacteria is quite different in several respects from the synthesis of cytoplasmic polysaccharides, for instance, glycogen: (a) the assembly of the macromolecules occurs in distinct stages which correspond to different intracellular localization;

(b) during some of these stages the biosynthetic intermediates are covalently attached to lipid carrier molecules; (c) some of the synthetic steps involve unusual mechanisms.

The first, cytoplasmic stage of peptidoglycan synthesis corresponds to the stepwise synthesis of the two parts of the eventual glycopeptide: part one is UDP-N-acetyl muramic acid with the pentapeptide (L-Ala-D-Glu-L-Lys or DAP-D-Ala-D-Ala) side chains already attached; part two is UDP-N-acetyl glucosamine. The second stage of biosynthesis takes place in or on the plasma membrane. Part one of the glycopeptide is transferred from UDP to a lipid carrier molecule, a C_{55} isoprenoid alcohol phosphate and all the subsequent steps of assembly occur with the reducing group of muramic acid attached (in pyrophosphate bond) to the lipid, called glycosyl carrier lipid (GCL)⁴². These subsequent steps include formation of the disaccharido-peptide (through linking up with the N-acetylglucosamine) and modification of the peptide side chain. These latter involve the attachment of short oligopeptide chains (composed of alanine, glycine or threonine) to the free amino group of the lysine or DAP residue of the disaccharido-peptide. The peculiarity of this reaction is that the amino-acid donor seems to be aminoacyl-transfer RNA, functioning in the apparent absence of ribosomes or mRNA⁴³. The third stage of this synthetic sequence is transport of the GCL-linked and modified disaccharido-peptide units (or, possibly, their oligomers) to some acceptor sites in the peptidoglycan layer of the surface. The final stage is incorporation into the old surface. Practically nothing is known about the mechanisms of transport. The only definite information we have about the mechanism of incorporation is that the glycopeptide units are added in covalent linkage to some acceptor sites (possibly through glycosidic bonds with the carbon atom 4 of some terminal glucosamine residue) in the old peptidoglycan network. A second and last reaction at present known is cross linking (by peptide bonds) of the peptide side chains of neighbouring glycopeptide units. The existence of cell wall growth zones in some bacteria (see later) suggests that the active acceptor sites of the peptidoglycan may also be clustered at the equatorial zone of the cell surface.

In LPS synthesis, the molecule is also made in two parts: the "core" region and the O-antigenic chains⁴⁴. The early (cytoplasmic?) stages of the synthesis of the former are not well understood, and in the case of the O-antigen the very first synthetic step already occurs in or on the plasma membrane. This is the transfer of galactose from UDP-gal to a GCL, an isoprenoid alcohol phosphate which seems chemically identical to the one functioning in peptidoglycan synthesis. All the subsequent reactions, the build-up of the trisaccharide, their polymerization and eventual linkage to the other half ("core") of the LPS, occur by membrane-bound enzymes and with the oligosaccharide chain attached to GCL.

The other part of *Salmonella* LPS, the so-called "core" region, is synthesized by stepwise transfer of sugar residues from UDP-linked precursors to the growing end of the oligosaccharide which also contains covalently bound lipid (the so-called lipid A). Each step is catalysed by a specific enzyme and the first indication that the core was made in a lipid membrane came from the discovery of a peculiar phospholipid requirement: the oligosaccharide would only accept a new sugar residue in the presence of a glycerophosphatide, containing unsaturated or cyclopropane fatty acids and a certain type of polar group. More specifically, the acceptor had to be "annealed" with the phospholipid by heating. On adding the appropriate enzyme protein to the lipid and oligosaccharide a ternary complex of these could be isolated by sucrose density gradient centrifugation.

These experiments were recently repeated in an *in vitro* monolayer system in order to approximate the *in vivo* conditions⁴⁵. A mixed monolayer film was constructed stepwise: acceptor oligosaccharide molecules were allowed to penetrate a film of phosphatidylethanolamine; next, the enzyme molecules were introduced in a similar fashion and finally radio-

active UDP-sugar was introduced in the subphase of the tricomponent film. Several striking observations were made. (1) In the monolayer, "annealing" of the acceptor and the P-lipid was no longer necessary for the attachment of a sugar residue. (2) While in the reaction occurring in suspension several hundred sugar units would incorporate per enzyme molecule, in the monolayer only about two. (3) Monolayers which were prepared with phospholipids inactive in the suspension assay were found impenetrable by the polysaccharide acceptor molecules.

Recent work in Osborn's laboratory (personal communication) has demonstrated that all the biosynthetic enzymes for the synthesis of both the "core" region and the O-antigenic chains of LPS are located in the "inner" (plasma) membrane. Pulse chase experiments showed that the biosynthesis of LPS molecules is completed in the plasma membrane and these molecules are then transported to the outer membrane apparently without the GCL. Nothing is known about the mechanism of transport.

Incorporation into the Cell Surface

The "anchoring" of various macromolecules into the appropriate pre-existing surface layer occurs by various types of lateral interactions with components of the "old" surface and we know very little in biochemical terms about these. The monolayer studies on LPS synthesis provided some suggestions concerning the types of lateral interactions which may also occur *in vivo* between lipid, polysaccharide and protein molecules sharing a common surface layer. One of these suggestions is the structural requirement in the lipid component for successful mixed film formation. The restriction of the activity of surface-bound enzyme leads to the proposal⁴⁴ that the synthesis of the core polysaccharide *in vivo* may occur by the diffusion of the incomplete polysaccharide through a properly arranged cluster of enzymes, each adding one sugar unit to the substrate. This would, of course, be reminiscent of other organelle-linked biosyntheses, such as ribosomal protein synthesis. Nothing is known about the organization of the components of outer membrane in the well-membrane junctions¹³, which must include clusters of virus receptor LPS molecules.

In the growth of the plasma membrane the various functional protein molecules cannot be arranged completely at random either, for proper functioning of some of these requires that they be in the close vicinity of one another. This must be, for example, the case with D-lactic dehydrogenase and transport proteins which derive energy from lactose oxidation⁴⁶. Clearly we cannot even start thinking in biochemical terms about how the topographic arrangement of specific proteins is brought about in such differentiated areas of the surface as flagella or periplasm.

There are numerous examples for specific interactions between lipids and proteins also during incorporation into the plasma membrane. While functional proteins (as well as bulk protein) can apparently incorporate into the membrane in the absence of lipid synthesis⁴⁷, such proteins may function inefficiently^{48,49}. In some cases this inefficiency can be corrected for by subsequent resumption of lipid synthesis⁴⁹. In the case of some membrane proteins at least, the newly made proteins tend to associate with lipid made at the same time. A fatty acid auxotroph of *E. coli* growing on oleic acid was briefly shifted to linoleic acid and induced for β -galactoside transport. On returning to the oleic acid medium, the galactoside transport rate of such cells at different temperatures was typical of linoleic-acid grown cells. Consistent results were found in the reverse experiment or if the same culture was induced for two independent transport systems. In each case, the properties of the permease indicated that some time during incorporation into the membrane newly made protein preferentially associated with lipid incorporated at the same time⁵⁰. Whether the peculiar (hydrophobic) properties of membrane-

bound enzymes always appear *in statu nascendi*, or whether they may acquire these in some post ribosomal event, perhaps by interaction with lipids in the membrane, is not known. In fact it is not even known if such membrane-bound enzymes are functional prior to incorporation into the membrane. Some of these proteins may be present in an inactive zymogen form while in the cytoplasm, similar to the case of several secretory enzymes in eukaryotic cells.

The mode of surface extension in the macroscopic sense has been approached by several experiments. In biochemical terms practically nothing is known about mechanisms of this process, thus the more biological term "growth" seems adequate. All the more appropriate is this term, since the problems of biosynthesis at this level merge with such fundamental cell biological problems as the control of cell division, mechanism of chromosome segregation and control of cellular morphology.

Experiments were designed to ask two separate but inter-related questions. (i) What is the size of the parental surface that is conserved during cellular growth and division? (ii) Do new components enter the pre-existing surface at random locations or within localized growth zones? The first question was approached in segregation experiments in which a specific surface component of the parent cell was labelled (with isotope or fluorescent antibody) and subsequently the distribution pattern of the label was determined among progeny cells by quantitative autoradiography or fluorescence microscopy. The first experiment of this sort was done in *E. coli* labelled with $^3\text{H-DAP}^{51}$. From six to eight generations of segregation the distribution of radioactivity in the progeny cells was random, implying that the parental peptidoglycan was broken up and passed on to progeny cells in no less than about 250 fragments. In a similar experiment with *E. coli* segregation of lipid label was followed. A distinct deviation from a random (Poisson) distribution of the label was observed between the sixth and eighth progeny generation⁵². This finding implies that the lipid containing parental surface layer (plasma membrane and/or outer membrane?) may be broken up to no more than about 250 units (a surface area of about $5 \times 10^4 \text{ nm}^2$) which would then be conserved during subsequent growth.

A variation of the experimental design in such studies exploits chain formation of bacteria: the labelled parental cell is put under conditions which allow cell division but prevent physical separation of daughter cells. The resulting "chain" of bacteria represents a linear clone with progeny cells lined up in a nice geometric arrangement. From the localization of label within such "chains" one can deduce the pattern of segregation⁵³.

In the Gram positive bacterium *Streptococcus pyogenes*, Cole and Hahn⁵⁴ and May⁵⁵ were first to demonstrate by an immunofluorescence technique the conservation of surface antigens (polysaccharide?) during growth. These experiments were reproduced in several other Gram positive bacteria⁵⁶ also and were confirmed by an autoradiographic method in the case of teichoic acid or pneumococcus⁵⁷.

Growth Zones

The simplest interpretation of a non-conservative segregation is that growth of the surface occurs at many points, while in conservative segregation growth may be restricted to one or few zones. While consistent with such interpretations, segregation experiments cannot prove zonal or multiple site growth. To answer this second problem requires different techniques. Direct evidence for the existence of growth zones was obtained in the case of streptococcal surface antigens (presumably polysaccharide)⁵⁶, M-protein⁵⁸, capsular polysaccharide and the choline containing teichoic acid of pneumococcus⁶⁰, by immunofluorescence or electron microscopic methods. It is interesting that a number of chemically distinct macromolecular cell components occupying different strata in the surface structure all enter the cell surface at the same equatorial growth zone.

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Network Thermodynamics

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The techniques of network theory are generalized to include irreversible thermodynamic systems. Complex nonlinear systems can be treated in this way in terms of a well-defined mathematical structure.

CLASSICAL thermodynamics is limited in that it deals only with the initial and final equilibrium states of a process; it provides no information about the dynamical behaviour between these states. Thermodynamics tells us where we have been and where we are, but not how we got there.

Nonequilibrium thermodynamics, as developed by Onsager and others¹⁻⁴, has been successful in correlating many physical, chemical and biological phenomena. It falls short of a complete dynamical theory, however, because it treats only the irreversible aspects of processes and is thus an algebraic theory restricted primarily to describing time-independent (steady) states. Moreover, the stringent restriction of linearity is placed on the admissible constitutive relations between the thermodynamic forces and fluxes, thus excluding many nonlinear phenomena which seem to dominate the dynamical behaviour of biological systems. Another serious limitation of the Onsager formalism is the difficulty of providing a macroscopic description when a system is complex; yet inhomogeneity and anisotropy are the hallmarks of organizational complexity in biological systems. In this article we attempt to resolve some of these difficulties by combining classical and irreversible thermodynamics with modern network theory.

Network Theory

Thermodynamics is a phenomenological theory and, as such, is a purely formal structure. It offers no "explanation" of physical events, but serves only to organize knowledge and establish relationships between quantities. Similarly, the principal purpose of the phenomenological theory proposed here is to provide an organizational framework for treating complex thermodynamic processes. The techniques developed here are especially well suited to the description of biological systems, where analysis is complicated by the nonlinearity of the individual dynamic processes, the organizational complexity of the system as a whole and the mathematical intractability of the resulting equations.

These problems are similar to those encountered in dynamical systems and control theory, where one particular application of nonequilibrium thermodynamics—electrical network theory—has been extremely successful. Circuit analysis is not usually considered as an application of nonequilibrium thermodynamics, no doubt because its specialized techniques seem quite foreign to the classical methods of thermodynamics. In fact, however, the network approach is quite general, and with modifications it can be applied widely to thermodynamic systems (see ref. 5). Indeed, the network approach to irreversible processes has several advantages. Not only does it provide a formalism, but it brings thermodynamics within the framework of modern dynamical systems theory, thus bringing to bear a great body of analytical tools on the problem of biological complexity. The technique described here is not, however, merely an alternative version of "equivalent circuit" modelling; rather, the objective is to exploit the underlying unity in the mathematical description of all dynamical theories⁶.

The network approach also makes it possible to construct a graphical representation for thermodynamic systems analogous to circuit diagrams in electrical network theory. Such network graphs are far more than pictorial representations of particular physical systems. Because the dynamical equations may be read algorithmically from the network graph, the diagrams are actually another notation for the equations themselves in much the same way as the operators of vector analysis are a more lucid notation for the component representation. In addition the network graph actually contains information not available in the bare differential equations—it reveals the system topology. This crucial aspect has been largely neglected in the treatment of thermodynamic systems. Yet the way in which a system is "hooked up" will impose a set of constraints on its behaviour which endow the system with its organizational character: a system of capacitors, resistors, and so on functions as a radio only if they are appropriately connected.

Underlying the network approach is the duality of the mathematical structures available for the description of dynamical systems: point set topology and algebraic or combinatorial topology. Continuum theories use vector calculus, whose operational structure arises from point set topology, to generate partial differential field equations. Combinatorial topology, on the other hand, describes the continuum by examining it at a finite number of specified points, giving rise to ordinary differential equations. Both point set topology and its discrete counterpart, algebraic topology, seek to describe the connectivity properties of the space in which the dynamical processes are described. In the network approach we "pull apart" the

continuum, revealing the implicit topological relations. For example, if we wish to describe the current and potential distribution on a conducting sheet, instead of trying to specify the entire distribution by continuous functions we could overlay the sheet with a network or mesh of a finite number of nodes and branches and tabulate the meter readings giving the current flow through each branch and the potential differences between each node pair. It seems reasonable that, as the mesh is made finer and finer, we can approach the actual continuum distribution to any desired degree of accuracy. In fact, in the limit of infinitesimal mesh size, the linear operators, represented by the connexion matrices of the network, become the differential operators of vector calculus^{7,8}. In this spirit, Kron and others have constructed network representations for practically all of the field equations of physics, from the Navier-Stokes equations to Schrödinger's equation⁹⁻¹⁴, and the technique has also been used to represent certain aspects of membrane function^{15,16}.

The general plan of this development of network thermodynamics involves three steps. First, constructing an isomorphism between the thermodynamic system and a topological or graphical structure. Second, imposing upon this graphical structure an algebraic or analytical structure equivalent to the equations of thermodynamics. Third, exhibiting the computing algorithm generated from the graphical representation.

State Variables and Constitutive Relations

The central device employed in network thermodynamics is the conceptual separation of "reversible" and "irreversible" processes. That is, we mentally reticulate the system into subsystems, each of which either stores energy reversibly or dissipates energy without storage¹⁷. Furthermore, we suppose that each subsystem or element is characterized by a finite number of ports, that is, interactions with its surroundings. Elements are frequently classified by their number of ports. (In circuit theory a 1-port is sometimes called a "2-terminal device"²⁶.) In addition, we define ideal energy bonds which are generalizations of perfectly conducting wires, infinitely stiff rods and other ideal "connectors" which transmit power instantaneously and without loss or storage from one element to another. For electrical circuits, these idealizations assume a concrete form: ideal capacitors and resistors are separate 1-port (2-terminal) physical devices. The separation of reversible and irreversible processes in, for example, a chemical reaction is, however, a purely mathematical device.

Before dealing with the first step we must define the dynamical variables used for the description of the system. Equilibrium thermodynamics postulates that there exists a unique state function, the internal energy $U(S, V, N_k, \dots) \equiv U(q_1, q_2, \dots, q_n)$, which is a function of the various thermodynamic displacements q_i such as the entropy S , the volume V , and the number of moles of the k th component N_k . Taking the differential of U and defining the conjugate potentials—temperature T , pressure p and chemical potentials μ_i —one obtains the Gibbs equation

$$dU = \sum_{i=1}^n \frac{\partial U}{\partial q_i} dq_i \equiv TdS - pdV + \sum \mu_i dN_i \quad (1)$$

Rather than attempting to obtain a dynamical theory from an equilibrium relation by dividing by dt , it makes more sense to go the other way: to start with a dynamical theory and require that it reduce to the correct equilibrium theory.

Most systems that can be analysed with the network approach share one common property: the rate of energy transmission, dissipation or storage is finite and may be expressed as a product of an "effort" or force variable, e , and a flow variable, f ; that is, energy rate (power) = ef . In electrical networks these variables are, of course, voltage difference and current; in mechanics: force and velocity; in diffusional processes: chemical potential difference and mass flow; in chemical reaction: affinity and rate of reaction; and so on.

By integrating e and f we can define two additional state variables: the generalized displacement,

$$q(t) \equiv q(0) + \int_0^t f(t) dt \quad (2)$$

and a generalized momentum,

$$p(t) \equiv p(0) + \int_0^t e(t) dt \quad (3)$$

For example, ξ , the advancement of a chemical reaction, is a generalized displacement variable, defined here by equation (2) as

$$\xi(t) = \xi(0) + \int_0^t J_r dt$$

where J_r —the reaction rate—is the flow variable.

As in electrical network theory, we associate two dynamical variables with each energy bond: a variable (f or q) which obeys a local conservation law (Kirchhoff's current law, KCL), and a variable (e or p) which is a continuous function (Kirchhoff's voltage law, KVL). The latter property is related to the local equilibrium postulate¹⁸.

In order to make predictions based on any phenomenological theory, information must be supplied about the system in the form of constitutive relations (equations of state, branch relations). These are obtained either experimentally or from a more detailed theory, such as statistical mechanics.

There are three kinds of energetic transactions possible: that is, three ways of integrating the equation $P = \mathbf{e} \cdot \mathbf{f} = \sum_{\text{ports}} e_i f_i$.

$$E_C(t) = \int_0^t \mathbf{e} \cdot \mathbf{f} dt = \int_{q(0)}^{q(t)} \mathbf{e} \cdot d\mathbf{q} \quad (4)$$

to give capacitive, or "displacement" energy storage,

$$E_L(t) = \int_0^t \mathbf{f} \cdot \mathbf{e} dt = \int_{p(0)}^{p(t)} \mathbf{f} \cdot d\mathbf{p} \quad (5)$$

to give inductive, or kinetic energy storage, and

$$E_R(t) = \int_0^t \mathbf{e} \cdot \mathbf{f} dt \quad (6)$$

to give energy dissipation.

To perform the first integration we require capacitive constitutive relations between the displacement and charge variables of the form

$$\mathbf{q} = \Psi_c(\mathbf{e}) \quad (7)$$

An ideal multiport element, which stores energy by virtue of a generalized displacement, will be called a capacitor, and denoted generically by C . (In instances of biological interest such a device may be a volume element which stores chemical energy due to a thermodynamic displacement.) From the constitutive relation (7) we obtain

$$\frac{d\mathbf{q}}{dt} = \frac{d\Psi_c}{d\mathbf{e}} \frac{d\mathbf{e}}{dt} \quad (8)$$

Defining the reversible flow on the capacitor:

$$\mathbf{f}_{\text{rev}} \equiv \frac{d\mathbf{q}}{dt}$$

and the incremental capacitance

$$C \equiv \frac{d\Psi_c}{d\mathbf{e}} \quad (9)$$

we obtain:

$$\mathbf{f}_{\text{rev}} = C \frac{d\mathbf{e}}{dt} \quad (10)$$

where e is the unique potential characterizing the capacitor. To illustrate this generalized notion of a capacitor we can consider the case of an ideal mixture for which the chemical potential of the i th component is $\mu_i = \mu_i^0 + RT \ln X_i$, where X_i is the mole fraction, μ_i is the chemical potential and μ_i^0 the reference potential of the i th component. By equation (9) the incremental capacitance is

$$C_i = \left(\frac{\partial N_i}{\partial \mu_i} \right)_{P,T,n_j} = \frac{N_i}{RT(1-X_i)} \approx \frac{N_i}{RT} \text{ for } X_i \ll 1 \quad (11)$$

where N_i , the number of moles of species i , is the displacement variable q and the effort, e , is $\mu_i - \mu_i^0$.

Energy may also be stored as a result of the relative motion of mass or charge (that is, kinetic or electromagnetic energy). In such cases, the second integration can be performed, given the constitutive relation $\mathbf{p} = \Psi_L(\mathbf{f})$. This type of energy storage device will be denoted by L , a generalized inductance. In mechanical networks the constitutive relation between momentum and velocity is merely the mass¹⁹⁻²¹.

Finally, for the dissipative element, denoted by R , we require the constitutive relation between e and f in order to compute the energy dissipation. For example, in a chemical reaction the effort, conjugate to the reaction flow, J_r , is the chemical affinity, A , which is related to J_r by the constitutive relation

$$A = \Psi_R(J_r) \quad (12)$$

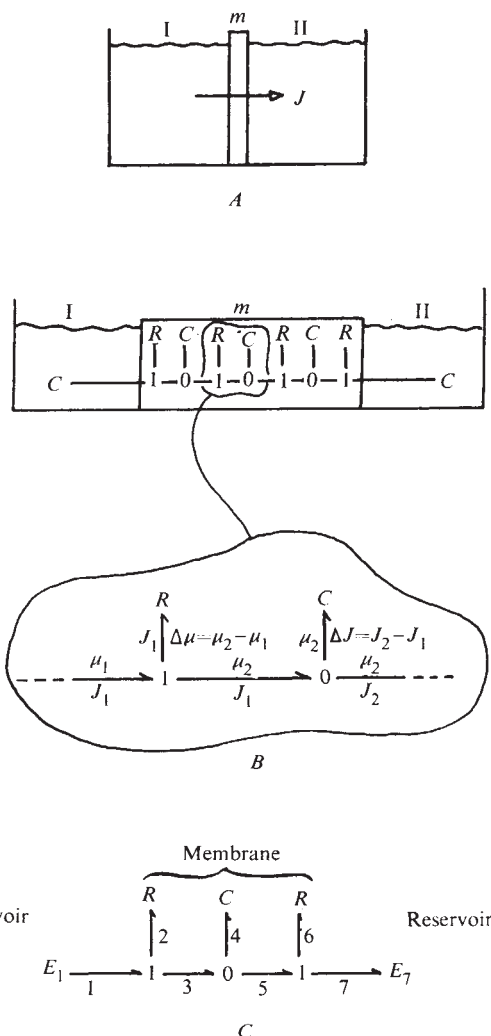


Fig. 1 Diffusion bond graph.

The incremental resistance R of a chemical process is

$$R \equiv \frac{\partial A}{\partial J_r} = \frac{\partial \Psi_R}{\partial J_r} \quad (13)$$

It is worth noting that as a chemical reaction proceeds, the free energy dissipated by the reaction is the difference between the free energy supplied by the reversible discharging of the local capacitors of the reactants and the free energy stored by the charging of the product capacitors.

As another example of the separation of reversible and irreversible processes, consider the case of membrane transport (Fig. 1A). A complete description of the system must include not only the dissipative processes but also the reversible discharge of permeant from compartment I, its concomitant reversible accumulation in compartment II and the concentration changes within the membrane itself. The latter aspect is central when analysing nonsteady transport across the membrane: for it is only in a steady state that the concentration in the membrane is time independent and the process may be treated as a pure irreversible phenomenon. On the other hand, during the course of a nonsteady flow, the membrane may gain or lose permeant so that the capacitance of the membrane itself must be considered.

The ideal elements (R , L , C)—plus one additional device to be introduced later—are sufficient to construct finite dimensional representations of most thermodynamic systems. Note that the letters R , L and C are only symbolic notations for the constitutive relations themselves. The existence of such functions is equivalent to the postulate of local thermodynamic equilibrium on which the validity of nonequilibrium thermodynamics rests. Moreover, we take as our definition of reversible and irreversible the existence of unique port constitutive relations (L , C) and (R), respectively. Fig. 2 shows the relation of the state variables to the constitutive relations.

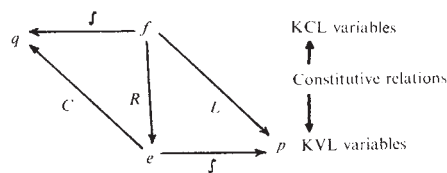


Fig. 2 State variables and constitutive relations.

Bond Graphs

The representation of dynamical systems other than electrical networks by linear graphs is a well established technique in engineering¹⁹⁻²¹. They quickly become unwieldy, however, and confusing for even moderately complex systems. In order to represent more general processes, in which many types of energy are involved, a more satisfactory graphical notation called bond graphs has been developed. This notation, devised by H. Paynter (see refs. 22-25), is particularly well suited for nonequilibrium thermodynamics. This generalization of linear graphs treats all energetic flows on an equal footing and hence provides an easily visualized notation for energy conversions and coupling.

In bond graphs we introduce a set of junctions that generalize the notion of series and parallel connexions, and that permit us to join the ports of the energy processing elements. These junctions may be considered as black boxes consisting only of connexions (connexion n -ports²⁶). Mathematically, these are simply a graphical notation for the set of linear constraint equations (KCL) and (KVL).

We require these junctions to be ideal in the sense that they neither store nor dissipate power: $\sum e_i f_i = 0$, where the sum is over all energy bonds incident on the junction.

First, a parallel or zero-junction, denoted by 0-junction:



is defined by $e_1 = e_2 = \dots = e_n$, or, since $\sum e_i f_i = 0$; $\sum f_i = 0$.

Second, a series or one-junction, denoted by 1-junction:



and defined by $f_1 = f_2 = \dots = f_n$, or since $\sum e_i f_i = 0$; $\sum e_i = 0$.

Note that each junction contains a statement of KCL (conservation), KVL (continuity) and conservation of energy, any two implying the third. A 0-junction may be regarded as a distribution point for flows; that is, flows split when incident on a 0-junction. Conversely, the effort splits or distributes when incident on a 1-junction. The one and zero-junctions lump together all flows and efforts that are equal.

To illustrate how a bond graph is constructed, consider the simple case of a single permeant diffusing through a homogeneous membrane (see Fig. 1A and refs. 24, 28). We assign capacitances to the membrane as well as to the reservoirs to allow for reversible charging and discharging of the permeant. Because dissipation accompanies each flow process, a resistive element must be assigned at both the entrance and exit of each volume element. The larger the number of volume elements considered, then the closer the ordinary differential equations will be to the continuum behaviour. By definition, there is a drop in chemical potential across the dissipative element, but no accumulation of permeant. Similarly, to each capacitive element we assign a unique chemical potential, and the flow must split in passing through the element since part of the flow goes for reversible charging. These conditions are fulfilled by inserting 1 and 0-junctions as shown in Fig. 1B. A consistent sign convention is the following: First, assume a positive power-flow direction; say from left to right as in Fig. 1B. This is indicated by appending a half-arrow to the energy bonds. Second, take power as positive into each element, so that, for example,

$$\begin{aligned} \rightarrow R \quad e &= \Psi_R(f) \\ \rightarrow R \quad e &= \Psi_R(-f) \end{aligned}$$

As a simple example of how the bond graph generates the governing state equations algorithmically, consider the relaxation time of a one-lump membrane. We will assume that the bounding compartments are so large that they may be effectively time independent, that is, an infinite capacitance is equivalent to a constant effort source, which we denote by E (Fig. 1C). For illustrative purposes all the constitutive relations are assumed to be linear. The constitutive relation for the membrane capacitor is therefore $C_4 e_4 = q_4$. Then

$$C_4 \frac{d}{dt} e_4 = \frac{d}{dt} q_4 \equiv (f_4)_{rev}. \quad (14)$$

According to the definition of a 0-junction $f_4 = f_3 - f_5$ while the 1-junctions imply that $f_3 = f_2$ and $f_5 = f_6$. The constitutive relation between dissipative flow and effort leads to $f_2 = e_2/R_2$ and $f_6 = e_6/R_6$, so that

$$C_4 \frac{d}{dt} e_4 = \frac{e_2}{R_2} - \frac{e_6}{R_6} \quad (15)$$

Again, according to the definition of the 1-junctions $e_2 = E_1 - e_3$ and $e_6 = e_5 - E_7$. Further noting that, for a homogeneous membrane, $R_2 = R_6$ are the membrane resistance R_m and C_4 is the membrane capacity C_m , we obtain:

$$\frac{de_4}{dt} = \frac{1}{R_m C_m} [(E_1 - e_3) - (e_5 - E_7)] \quad (16)$$

Reverting to thermodynamic notation and identifying E_1 and E_7 with the chemical potentials μ^I and μ^{II} of the reservoirs, we may define

$$\langle \mu \rangle \equiv \frac{E_1 + E_7}{2} = \frac{\mu^I + \mu^{II}}{2} \quad (17)$$

where $\langle \mu \rangle$ is the average chemical potential in the containers. Further, since $e_3 = e_4 = e_5 = \mu_m$, the chemical potential of the permeant in the membrane, the last equation leads to the relaxation expression

$$\frac{d\mu_m}{dt} = \frac{2}{R_m C_m} [\langle \mu \rangle - \mu_m] \equiv \frac{\langle \mu \rangle - \mu_m}{\tau_m} \quad (18)$$

The relaxation time for the membrane process

$$\tau_m = \frac{R_m C_m}{2} \quad (19)$$

has the expected form of an RC time constant familiar from network theory. The magnitude of R_m evaluated for an ideal permeation process is

$$R_m = \frac{RT\Delta x}{D_m (N_i/V)}$$

where D_m is the diffusion coefficient within the membrane and Δx the membrane thickness. The volume V is here the volume of the membrane per unit area or $V = \Delta x \cdot 1 \text{ cm}^2$, and hence the ideal membrane capacity according to equation (11) is

$$C_m = \frac{(N_i/V) \Delta x}{RT}$$

Inserting the magnitudes of R_m and C_m into equation (19) we regain the Einstein equation

$$\tau_m = \frac{(\Delta x)^2}{2D_m} \quad (20)$$

Since R is experimentally determined at steady state while C is obtained at equilibrium, only equilibrium and steady state measurements are required to characterize the dynamic behaviour of systems in network thermodynamics.

The important point here is that the dynamical equations, linear or nonlinear, for arbitrarily complex systems, are generated algorithmically from the bond graph. Therefore it is a simple matter to design a computer program that will accept the bond graph as its input and then compute the dynamical behaviour directly from the graph without dealing with the differential equations explicitly. In most cases the complexity of the system precludes analytical solutions in any event, so that it is easier to deal directly with the more intuitive graphical representation.

Coupled Phenomena

In order to treat energetic coupling and conversion in irreversible processes, we introduce an additional ideal element: a 2-port device that acts as an ideal converter or transducer. We denote it by:

$$\begin{array}{c} e_1 \searrow T^r \quad D^r e_2 \\ f_1 \quad \quad \quad f_2 \end{array}$$

and define it by the equations:

$$\begin{bmatrix} e_1 \\ f_1 \end{bmatrix} = \begin{bmatrix} r & 0 \\ 0 & -1/r \end{bmatrix} \begin{bmatrix} e_2 \\ f_2 \end{bmatrix} \quad \text{or} \quad \begin{array}{l} e_1 = r e_2 \\ f_1 = -1/r f_2 \end{array} \quad (21)$$

We see from the defining equation that the ideal transducer has two properties: first, it neither stores nor dissipates energy; viewed as a mapping from input space, (e_1, f_1) , to output space

(e_2, f_2) , $e_1 f_1 + e_2 f_2 = 0$. Second, it is a reciprocal device since its constitutive relation is a symmetric matrix.

The factor r is called the transducer modulus and includes the conversion units from the energy form on side 1 to the energy form on side 2. The modulus r may also be a function of other state variables in the system, and in this fashion we may incorporate pure signal flows and parametric feedback into thermodynamics^{24,25}. The transducer (TD) generalizes the notion of the ideal lever and transformer familiar from elementary physics. It is merely a pictorial representation of a set of constraint equations (and units conversion) on e and f , analogous to the 0 and 1-junctions.

To illustrate the use of the transducer to represent thermodynamic coupling let us consider the coupled diffusion of substances A and B passing a membrane. It is assumed that the two species interact according to the following requirements. First, their coupling is dissipative, and second the coupling interaction depends on the relative motion of the two species.

The coupling structure shown in Fig. 3A is easily seen to fulfil these requirements; it is represented by the coupling resistance R_c and also by the 0-junction. The diffusing species clearly must be coupled through the 1-junction, because the energy exchange between the species occurs only during flow. As shown elsewhere²⁵, this bond graph reproduces the equations corresponding to the usual frictional model of diffusion coupling²⁹⁻³¹.

An alternative coupling between the diffusional flows of A and B is through a chemical reaction in which, for example, substance A is converted into substance B.

Here the transducer element TD is employed again, not for the representation of pure energy conversion, but for the stoichiometric conversion of a species in a chemical process. The flow of a chemical reaction J_r is

$$f \equiv J_r = \frac{1}{v_i} \frac{dN_i}{dt} \text{ by KCL} \quad (22)$$

and the associated effort is the affinity

$$e \equiv A = - \sum v_i \mu_i \text{ by KVL} \quad (23)$$

where v_i = stoichiometric coefficient of species i .

Let us now allow the diffusing species in the previous example to react chemically with one another as they migrate across the membrane: $v_A A \rightleftharpoons v_B B$. We must couple the local capacitors of species A and B through a reaction 2-port. The reticulation of this 2-port for near equilibrium reactions is shown in Fig. 3B. The reticulation for reactions far from equilibrium requires a profound modification, dealt with in ref. 25. It is easy to see from the definitions of each element that the structure shown corresponds exactly to the correct thermodynamic equations for a chemical reaction. A reaction is always accompanied by dissipation, accounted for in the constitutive relation of R_r , which in general is nonlinear. The expression for the affinity can be written in the form of KVL: $A + \sum v_i \mu_i = 0$, which defines the 1-junction of the reaction 2-port. The moduli of the transducers are then the stoichiometric coefficients.

A straightforward calculation verifies that the bond graph algorithm produces a finite difference equivalent of the diffusion-reaction field equations^{24,25}. Moreover, the bond graph allows a clear topological separation of the reversible and irreversible processes accompanying a chemical reaction. The reversible part clearly must be present in reaction as well as in diffusion, in order to treat non-stationary behaviour.

The network technique described above has been used by us to describe several experimental systems. These include diffusion-reaction studies, including facilitated and active transport, rectification properties of complex membranes and relaxation oscillations in coupled membrane systems^{25,32}. In all cases good agreement between the bond graph solution and the experimental results was obtained.

Once the network representation for thermodynamics has been established, a large body of theory becomes available,

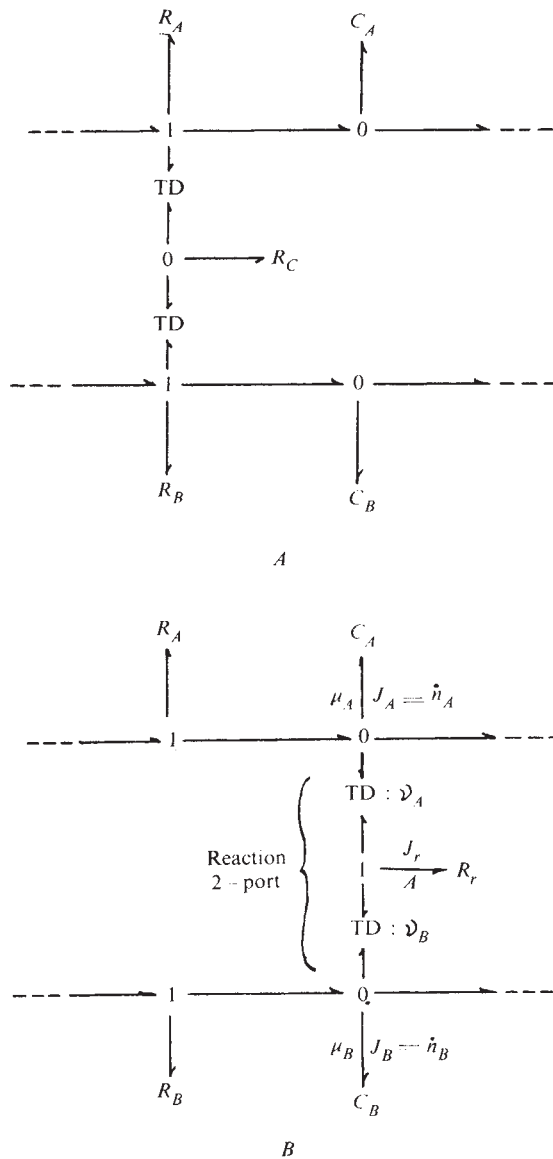


Fig. 3 A, Diffusion coupling; B, reaction coupling.

permitting many previous results to be viewed from a unified perspective. One of the central unifying conclusions in network theory is Tellegen's theorem³³. It is remarkable that virtually every energy distribution theorem for thermodynamic networks as well as several results from nonequilibrium thermodynamics may be derived starting from this powerful theorem^{34,35}. The reason for its generality is that it is a purely topological result, based only on KCL and KVL, and is independent of any assumptions concerning either the constitutive relations or stationarity. Since 1883, when Heaviside first used a form of Tellegen's theorem to derive Maxwell's minimum heat theorem (minimum entropy production), versions of the theorem have reappeared in various forms from time to time in the engineering and mathematics literature. However, the first to recognize and exploit its generality and usefulness was B. D. H. Tellegen³³. For an account of its historical development and references to continuum versions and applications of Tellegen's theorem, see ref. 35. Here we restrict ourselves to a brief heuristic discussion of this fundamental theorem from a thermodynamic viewpoint.

Network thermodynamics, like electrical network theory, considers only systems in which the sources of interest (reservoirs) are included in the system. The sources are regarded as system elements which interact with the rest of the system

through specified ports. Thus, in the membrane example, the compartments adjacent to the membrane were considered as an integral part of the system. The systems considered here are therefore closed and may be assumed isothermal and isobaric. In accord with the requirements of the second law of thermodynamics, the free energy of the system, G , as determined in the capacitative elements, is found to decrease with time, or

$$\frac{dG}{dt} < 0 \quad (24)$$

This decrease is attributed to the dissipative processes and indeed dissipation is identified with $-dG/dt$. An adequate measure of irreversibility is the dissipation function

$$\varphi \equiv T \frac{d_i S}{dt} > 0 \quad (25)$$

where $d_i S/dt$ is the positive definite entropy production. From a classical point of view we may say that the energy dissipated by all irreversible processes proceeding in a closed, isothermal and isobaric system is equal to the decrease in free energy, that is,

$$\frac{dG}{dt} + \varphi = 0 \quad (26)$$

Equation (26) may be cast in the suggestive form

$$\varphi + \frac{dG}{dt} = \sum_{\text{irrev.}} e_i f_i + \sum_{\text{rev.}} e_j f_j = 0 \quad (27)$$

which is the thermodynamic form of Tellegen's theorem. Equation (27) may be given a striking geometrical interpretation by defining two state vectors

$$\begin{aligned} \mathbf{f} &\equiv \underbrace{(f_1, \dots, f_m)}_{\text{irrev.}}; \underbrace{(f_{m+1}, \dots, f_n)}_{\text{rev.}} \\ \mathbf{e} &\equiv \underbrace{(e_1, \dots, e_m)}_{\text{irrev.}}; \underbrace{(e_{m+1}, \dots, e_n)}_{\text{rev.}} \end{aligned} \quad (28)$$

Therefore,

$$\mathbf{e} \cdot \mathbf{f} = 0 \quad (29)$$

The scalar product of $\mathbf{e}$ and $\mathbf{f}$ is equivalent to equation (27), and hence equation (29) may be interpreted as an orthogonality condition between the flow and effort state vectors. That is, the $2n$ dimensional state space defined by all the efforts and flows is decomposed into the direct product of two orthogonal subspaces. No assumptions of linearity or steady state are required; the orthogonality condition holds at each instant of time regardless of the nature of the system^{7,33,35}.

Reciprocity and Onsager's Relations

In nonequilibrium thermodynamics, if linear constitutive relations are assumed, reciprocity appears as the symmetry of the matrix relating the various forces and fluxes. In this context it is usually called Onsager reciprocity. More generally, if the port quantities are related by a nonlinear function

$$\mathbf{e} = R(\mathbf{f}) \quad (30)$$

reciprocity is the symmetry of the Jacobian of R :

$$J_R = J_R^T \quad (31)$$

where J_R^T is the transpose of matrix $J_R = (\partial e_i / \partial f_j)$.

Mathematically, reciprocity is merely an integrability condition on the constitutive relations, assuring the existence of a unique real valued function of the port parameters, which, when differentiated, yields all the constitutive relations. In equilibrium thermodynamics, the existence of such a state function is postulated—it is the internal energy or its Legendre transforms

and the resulting reciprocity conditions are the well known Maxwell relations. Physically, reciprocity of a system assures us that if we vary the input on one energetic port while observing the effect at another port, we may then reverse the position of input and observer and expect to obtain symmetrical measurements—at least up to small signal. That is, there exists a unique scalar function which is able to account for variations in all the port parameters.

For thermodynamic systems represented by bond graphs consisting of reciprocal elements, reciprocity is assured due to a theorem proved by Brayton²⁶ which states that any interconnection of reciprocal elements—that is, elements characterized by a symmetrical Jacobian matrix of constitutive relations—is reciprocal. Note that each 1-port is trivially reciprocal, since its Jacobian is just a number. Moreover, it can be shown that "connexion n -ports (junctions) are also reciprocal²⁶. The proof of the overall reciprocity of the system employs only Tellegen's theorem and the topological statements of conservation (KCL) and continuity (KVL) that have been imposed on the system by definition^{24,27}.

It is important to note that the extended definition of reciprocity given here includes both reversible and irreversible processes, and is valid when the functional relationship between forces and flows is nonlinear. A system composed of reciprocal components will exhibit only "trivial" dynamic behaviour, that is, monotonic decay to a stationary point. Oscillations and amplification are not possible with reciprocal systems. Hence biological systems are generally not reciprocal.

State Equations

For finite dimensional dynamical systems the equations of motion are usually given in the state space form: $\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}, \mathbf{u})$; where $\mathbf{x}(t)$ describes the trajectory in state space and $\mathbf{F}$ is the vector field propelling the state point. It is of paramount importance in dynamical theories to have a general prescription for the vector field $\mathbf{F}$. For instance, in classical mechanics, the canonical equations of Hamilton describing the evolution of any conservative mechanical system have the form:

$$\mathcal{J} \mathbf{x} = \nabla H \quad (32)$$

where

$$\mathcal{J} = \begin{bmatrix} \mathbf{0} & \mathbf{I} \\ -\mathbf{I} & \mathbf{0} \end{bmatrix}, \quad \mathbf{x} = \begin{bmatrix} \mathbf{q} \\ \mathbf{p} \end{bmatrix}, \quad \nabla H = \begin{bmatrix} \partial H / \partial \mathbf{q} \\ \partial H / \partial \mathbf{p} \end{bmatrix}$$

For a wide class of nonlinear reciprocal networks, the Brayton-Moser equations²⁴ have an equally elegant form:

$$\mathcal{J} \dot{\mathbf{x}} = \nabla \mathcal{P} \quad (33)$$

Where $\mathcal{J}$ is a metric obtained from the reversible elements,

$$\mathcal{J}_{ij} = -\sum L_{ij}(\mathbf{f}) df_i df_j + \sum C_{ij}(\mathbf{e}) de_i de_j$$

and $\mathcal{P}$ is a mixed potential obtained from the irreversible constitutive relations. The differential equations obtained earlier for the transient membrane diffusion are a simple example of these equations. For nonreciprocal dissipative systems, the state equations are not a gradient flow, and the Brayton-Moser-Smale equations take the form²⁵:

$$\mathcal{J} \dot{\mathbf{x}} = \omega \quad (34)$$

where ω is a nonintegrable differential form.

A large class of irreversible thermodynamic systems are described by these equations, and hopefully they will prove as valuable for thermodynamic systems as Hamilton's equations have been for point particle mechanics.

The techniques of network theory have been generalized to include a large class of irreversible thermodynamic systems. This approach has several advantages. First, it is capable of treating nonlinear, nonsteady systems of great complexity that include coupling and feedback effects. Second, an intuitive graphical representation is available. Third, a computing algorithm is generated enabling the equations of motion to be read directly from the graph. Finally, a well-defined mathe-

mathematical structure emerges, paralleling the modern axiomatic development of dynamical systems and network theory, which proves a unified perspective and generalization of previous results in nonequilibrium thermodynamics.

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Rotating Relativistic Ring

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Consideration of a rotating ring sheds light upon the problem of the rotating disk recently discussed in *Nature* by several authors and shows the disk problem to be more difficult than it appears.

THERE has recently been appearing in *Nature* an interesting correspondence about the relativistic treatment of a rotating disk¹⁻⁶. As the writers recall, the problem goes at least as far back as 1909 when Ehrenfest formulated a paradox on the inference that at any place in the disk lengths in the direction of motion would suffer the FitzGerald-Lorentz contraction while lengths perpendicular to this would be unaffected by the motion. This inference is incorrect, but the reason seems not to have been stated explicitly in the correspondence.

The problem is of peculiar interest, in the context of the discussion, only for the case of what may be called a "rigid" disk. In relativity theory, however, no disturbance may be propagated through matter with more than the speed of light c . Consequently in relativity theory there cannot exist anything

like a classical rigid body, in which all disturbances are propagated instantaneously. Of course, were it possible to have a body in which all disturbances are propagated with speed c , it would be natural to regard this as the analogue of the classical rigid body and to proceed accordingly. Actually, however, it appears to be impossible to select a self-consistent set of elastic constants so that even all infinitesimal disturbances, compressional, transverse and torsional, travel with speed c . In fact, there is as yet no satisfactory relativistic treatment of a two dimensional or three dimensional "rigid" body. Probably there are, indeed, many possible choices depending on the kind of disturbance for which the speed of travel is to be maximized. In this situation, it is clear that the problem of the rotating "rigid" disk is very far indeed from having yet been solved.

The solution of even the problem of a rotating "rigid" ring seems not to have yet been given. However, this may be treated as an application of the theory of the relativistically rigid rod, which Hogarth and McCrea⁷ (HM) gave many years ago. In this article I seek to solve the ring problem, and I consider briefly also the problem of the rotating rigid rod. In the light of this work, I then discuss the problem (but not its solution!) of the rotating disk.

As previous authors have remarked, since gravitation is not involved, only special relativity is concerned.

Rigid Ring

In HM we discussed a uniform straight "rod" that has the maximum degree of longitudinal rigidity permitted by relativity theory. We treated it as a one dimensional body and, as we remarked, nothing corresponding to flexural rigidity makes its appearance in one dimensional problems. So I may now suppose the ends of the rod to be joined so as to make it into a ring.

The intrinsic properties of the material, which I shall call the wire, are then the same as before. When the wire is at rest in an inertial frame under tension T , let L be the length and m the mass per unit length, and let L_0, m_0 be the values when $T=0$. From HM (3.1), (3.2) we have

$$T = \frac{1}{2} m_0 c^2 [1 - (L_0/L)^2], \quad m = \frac{1}{2} m_0 [1 + (L_0/L)^2] \quad (1)$$

Ring in Rotation

Let S be an inertial frame and let the wire be in a plane fixed in S ; let the wire be in a state of steady rotation such that it forms a circle with centre O , fixed in the plane, and with radius a , and such that every particle of the wire is moving with speed V along the circle. We may think of the ring as moving in contact with a fixed smooth plane over a fixed circle drawn on the plane. This circle may be graduated in a scale of length; standard clocks synchronized in S in the standard fashion may be situated along the circle. Any particle P of the moving ring may be marked, so that its velocity in S may be observed. If such a particle also carries a standard clock, we postulate that this clock measures proper time in the history of P . This is the usual "clock hypothesis" in the usual formulation of special relativity. If, when the moving clock is passing a fixed clock that reads zero, it also reads zero, then when it is passing a fixed clock that reads t , the moving clock reads $\beta^{-1}t$ where $\beta = (1 - V^2/c^2)^{-1/2}$. This follows at once by calculating the interval along the world-line of P between the two events.

Let $l = 2\pi a$ be the length of the wire, measured in S ; it is by definition the length of the fixed circle along which the whole length of the wire lies at any given instant in S . Then the proper-length of the wire L is

$$L = \beta l \quad (2)$$

This follows directly from the FitzGerald-Lorentz contraction, or by calculating the orthogonal interval between the world-lines of two neighbouring particles of the wire, or by considering light-travel times measured by an observer moving with a particle like P (see later).

In HM the relativistic equation of motion (4.2) in the inertial frame concerned states

$$\beta^2(m - T/c^2) \times \text{acceleration} = \text{force per unit length} \quad (3)$$

The only factor that may be unexpected is $m - T/c^2$, rather than simply m ; HM remarked that its correctness was checked by the fact that the equation gives c for the speed of wave propagation for all values of T . In the present case, the acceleration is V^2/a towards O and the force per unit length on any element of the wire is T/a as can be seen by resolving the tensions at the two ends of the element along the radius through its midpoint. Then (3) gives

$$(1 - V^2/c^2)^{-1} (m - T/c^2) V^2 = T \quad (4)$$

Using (1), (2) we then find from (4)

$$T = (1 + V^2/c^2)^{-1} V^2 m_0 \quad (5)$$

$$m = (1 + V^2/c^2)^{-1} m_0 \quad (6)$$

$$L = (1 + V^2/c^2)^{1/2} (1 - V^2/c^2)^{-1/2} L_0 \quad (7)$$

$$mL = (1 - V^4/c^4)^{-1/2} m_0 L_0 \quad (8)$$

$$l = (1 + V^2/c^2)^{1/2} L_0 \quad (9)$$

Thus $a = (1 + V^2/c^2)^{1/2} A_0$ where A_0 is the radius of the ring at rest.

Check on First Approximation

Before interpreting the foregoing results, it is instructive to obtain a first approximation by elementary methods. In HM we note that for small extension the wire obeys Hooke's law with modulus λ where $\lambda = m_0 c^2$, which it must do if small disturbances are propagated along it with speed c . So we now suppose that $V \ll c^2$ in which case we may use this approximation. We find directly from classical mechanics $T \approx m_0 V^2$. So the proper length of the wire is by Hooke's law

$$L = (1 + T/\lambda) L_0 \approx (1 + V^2/c^2) L_0 \quad (10)$$

To the same order (2) gives

$$l \approx (1 - \frac{1}{2} V^2/c^2) L \quad (11)$$

Combining (10), (11) again to the same order

$$l \approx (1 + \frac{1}{2} V^2/c^2) L_0 \quad (12)$$

It is seen that these very elementary results agree with those of the previous section to order V^2/c^2 .

Interpretation

Equation (12) shows from elementary mechanics that the most rigid possible ring allowed by relativity theory must be seen to expand when set in rotation relative to an inertial frame. From (9), the precise expansion factor is $(1 + V^2/c^2)^{1/2}$.

As V increases from zero to c , the radius increases from A_0 to $\sqrt{2}A_0$.

Once we see that the radius must begin to increase when the ring is set in rotation, we can see that the result found is qualitatively the only one that it is reasonable to expect. For if the radius begins to increase it is only natural to suppose that it will not decrease again as it is caused to rotate still faster. So as $V \rightarrow c$ the radius must tend to a finite limit greater than A_0 or must tend to infinity. But it would make no sense mechanically for an originally finite ring to be spun out to an infinite extension at a zero angular velocity!

The other features also are what we might expect on general grounds. As $V \rightarrow c$ the proper-length tends to infinity, and T, m tend to the corresponding limiting values.

The old argument was that an inextensible ring would, by definition, retain its proper-length and so would actually shrink to a smaller radius when set in motion. On the face of it, this seems absurd; we see that it is absurd because there can be no such thing as an inextensible ring.

At the same time, it might seem that some of the factors containing V appear somewhat "artificial". However, we have to appreciate that the case of rotation is quite artificial so far as rigidity properties are concerned, and so we have no cause to expect particularly elegant formulae. The one thing we ought to expect is that if we have two rigid rings of the same radius, we should not be able to make them more or less rigid by joining them together. This is borne out by the absence of m from the formulae for L and l .

Rotating Rigid Rod

Let us now suppose that our original rigid rod is rotating about one end fixed at O in the frame S ; suppose that it moves in a plane and that it is "straight" in a suitably defined sense; let ω be its (uniform) angular velocity in S . If P is any particle of the rod, let $OP = r$ where $r = r_0$ when $\omega = 0$. Since every part of the rod moves at right angles to itself in S , we may treat r as a distance in S and also as proper-distance along the rod. Thus the speed of P in S is $v = r\omega$. For given ω the distance $r = r(r_0)$ is a function of r_0 only, such that $r(0) = 0$. As before, let L_0 be the undisturbed length of the rod, and let $L = r(L_0)$ be its length when rotating; we write $V = L\omega$ for the tip-speed of the rod.

In this case m, T are functions of r , and in place of (1) we now have

$$T(r) = \frac{1}{2} m_0 c^2 [1 - (dr_0/dr)^2], \quad m(r) = \frac{1}{2} m_0 [1 + (dr_0/dr)^2] \quad (13)$$

and as a boundary condition we require $T(L) = 0$. The equation of motion (3) now becomes

$$\beta^2 (m - T/c^2) r \omega^2 = -d(T/dr) \quad (14)$$

where $\beta = (1 - v^2/c^2)^{-1/2}$. Using (13), this gives a second order differential equation for $r(r_0)$. Solving it in accordance with the boundary conditions and using the solution in (13), it is found that

$$\omega r/c = \sin[(\omega r_0/c)(1 - \omega^2 L^2/c^2)^{-1/2}] \quad (15)$$

whence, in particular, putting $r_0 = L_0$,

$$\omega L_0/c = (1 - V^2/c^2)^{1/2} \sin^{-1}(V/c) \quad (16)$$

$$T = \frac{1}{2} m_0 \frac{(L^2 - r^2)\omega^2}{1 - r^2\omega^2/c^2} \quad (17)$$

$$m = m_0 \frac{1 - \frac{1}{2}(L^2 + r^2)\omega^2/c^2}{1 - r^2\omega^2/c^2} \quad (18)$$

These results may be verified by direct substitution in (13), (14).

As before, we may also check these to the first order in v^2/c^2 by classical mechanics applied to a uniform rod having modulus $\lambda = m_0 c^2$. Elementary classical treatment yields

$$\begin{aligned} \omega r/c &= \sin(\omega r_0/c) \sec(\omega L_0/c) \\ \omega L/c &= \tan(\omega L_0/c) \\ T &= m_0 c^2 [\cos(\omega r_0/c) \sec(\omega L_0/c) - 1] \\ m &= m_0 \cos(\omega L_0/c) \sec(\omega r_0/c) \end{aligned}$$

If $\omega L_0 \ll c$, these give to order v^2/c^2

$$r \approx r_0 [1 + \frac{1}{2}(L_0^2 - r_0^2)\omega^2/c^2] \quad (19)$$

$$L \approx L_0 (1 + \frac{1}{2}\omega^2 L_0^2/c^2) \approx L_0 (1 + \frac{1}{2}V^2/c^2) \quad (20)$$

$$T \approx \frac{1}{2} m_0 (L_0^2 - r_0^2)\omega^2 \quad (21)$$

$$m \approx m_0 [1 - \frac{1}{2}(L_0^2 - r_0^2)\omega^2/c^2] \quad (22)$$

It is clear that equations (15)–(18) give the same results to this order.

At the other extreme we see from (16) that as $V \rightarrow c$ we have $L \rightarrow \infty$ and $\omega \rightarrow 0$; also from (17), (18) $T \rightarrow \frac{1}{2} m_0 c^2$, $m \rightarrow \frac{1}{2} m_0$ in agreement with (1) when $L \rightarrow \infty$.

If (16) be regarded as an equation for ω as a function of V , or as a function of L , then it is found that ω has a maximum for a particular value of V between 0 and c , and for a particular value of L between 0 and infinity, and ω tends to zero at the ends of the interval. For any intermediate value of ω there are two possible values of V and of L . All this behaviour is plausible on general grounds. As regards infinite extension in S , the difference between the cases of the rotating ring and the rotating rod is due to the fact that in S the ring is everywhere moving along its length whereas the rod is everywhere moving at right angles to its length. Thus, in particular, the ring can have infinite proper-length but finite relative length when its speed tends to c while the rod must have infinite length but zero angular speed in the limit when its tip-speed tends to c .

Discussion

Comparing (9), (16) it is seen that for given V the resulting values of l/L_0 and of L/L_0 are quite different, and from (12), (20) it is seen that they are different even to the first order in V^2/c^2 . If a rigid wheel is made of a rigid circular ring with rigid rods as spokes, then when it rotates the rim and the spokes will react on each other, so they cannot behave precisely as we have calculated for the cases in which they rotate independently. That is at any rate the way in which they will tend to behave, however. Thus the rim and the spokes tend to change their lengths in different ratios, whence it is to be inferred that the wheel cannot remain circular. This seems

to be the nearest we can get at present to solving the problem of the rotating disk.

There are further considerations that render the problem more complicated than it might appear even after noting the difficulties already mentioned. One is that, while axial symmetry is naturally specially significant in regard to rotation, the case of a disk of uniform thickness is no more special than that of a disk whose thickness depends on the radial distance r . For, as we see from a relation like (18) in the case of a uniform rod, uniformity is in any event lost as a result of the rotation itself. Thus there is no uniquely significant problem of "the" rotating disk.

Another complication concerns the means of setting a system in motion and the state that may be treated as one of steady rotation. This cannot be investigated here. But the simple cases of steady motion of the ring and the rod do appear to be perfectly possible physically. On the other hand, the motion considered, for example, by Weinstein⁶, whatever its significance, is not a state of steady motion.

Here it may be remarked that another interesting problem that has not yet been solved, but whose solution would be highly instructive, is that of an infinitely long rotating "rigid" circular cylinder.

Inertial Frames

The chief value of the sort of problem here considered is that it exhibits the significance of inertial frames in relativity theory. An inertial frame in special relativity is a freely moving, non-rotating, rigid body. In such a frame a rigid measuring rod has its usually assumed properties. Special relativity deals only with such frames because they are the only physically possible "frames" allowed by the theory. This is for the simple physical reason that the theory cannot admit undeformable bodies. If an accelerated observer tries to use a rigid measuring rod, the behaviour of the rod would be hopelessly confusing; it would depend on the point of the rod at which it is held as well as on what had been happening to the rod beforehand.

On the other hand, if a problem can be solved using any inertial frame, then it is possible to say what an accelerated observer will observe. For the behaviour of the required light-signals may be worked out using the inertial frame; in particular, the proper-times of arrival and departure of signals at the observer can be calculated. Provided the observer may be assumed to carry the "proper-clock" previously mentioned, the results are observable by him.

As opposed to this, observable results cannot in general be obtained by means of coordinate transformations. In particular, the "rotating coordinates" discussed in the correspondence referred to cannot have any direct physical meaning. It is essential to appreciate that this is a consequence of the basic physical restriction that matter cannot transmit effects with speed greater than c . The difficulty is not produced by any limitation—physical or mathematical—of special relativity as such. In fact the situation is exactly the same in general relativity except that, if a true gravitational field is present, then any inertial frame has only a local significance.

All this has to do with the principles of the theory. In practical applications, the classical notion of a rigid body is normally an adequate approximation. And when it is otherwise, then any modification would result from classical deformability. The relativistic limit of "rigidity" would never be approached by real material bodies.

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LETTERS TO NATURE

PHYSICAL SCIENCES

Cracking of Lunar Mare Soil

THE tendency of lunar soil to break into clods when disturbed was recognized from Surveyor 1 photographs^{1,2}. Pictures of disturbances produced in bearing tests with the Surveyor 3

soil mechanics surface sampler³ suggested to some observers that the soil layer in Oceanus Procellarum tends to crack into thin flat "tiles" (Figs. 1*a* and 2*a*) and, therefore, that it consists of a thin, rather rigid crust over a softer substrate. Pictures of areas disturbed by the Apollo 11 closeup camera in Mare Tranquillitatis (Fig. 3*a*) and by the Apollo 12 lunar module descent engine in Oceanus Procellarum conveyed a similar impression^{4,5}. None of the authors of these works were misled,

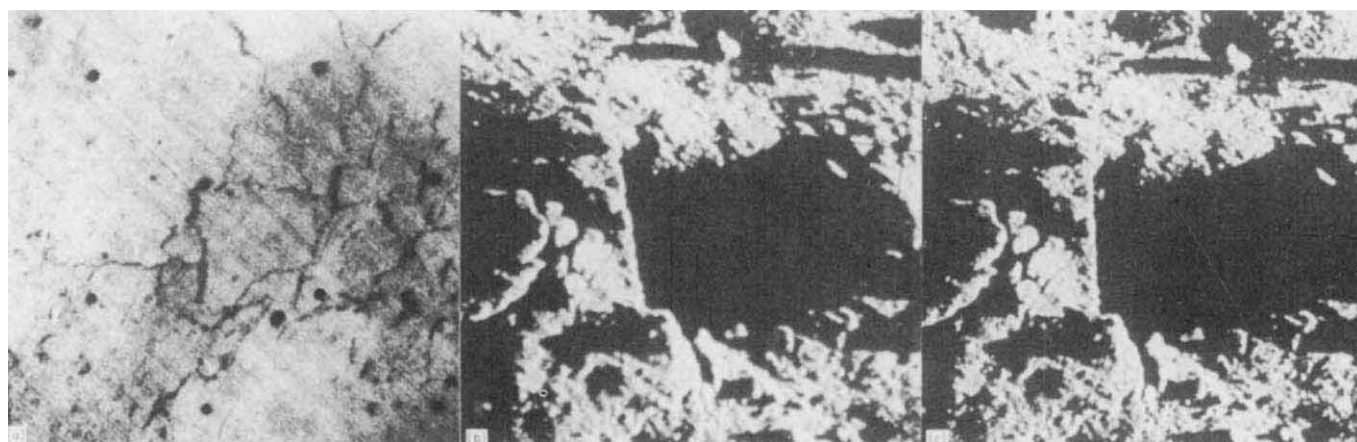


Fig. 1 Lunar surface disturbed by bearing test made with Surveyor 3 soil mechanics surface sampler (bearing test No. 2). *a*, Portion of picture made with Surveyor 3 television camera April 27, 1967, at 08 : 56 : 45 UT. View taken from west, rotated to match *b* and *c*, which are portions of photographs made with Apollo 12 hand-held camera on November 20, 1969, about 06 : 30 UT. View from south. *b* and *c* form a stereopair. (From NASA photographs AS 12-48-7106 and AS-12-48-7107.)

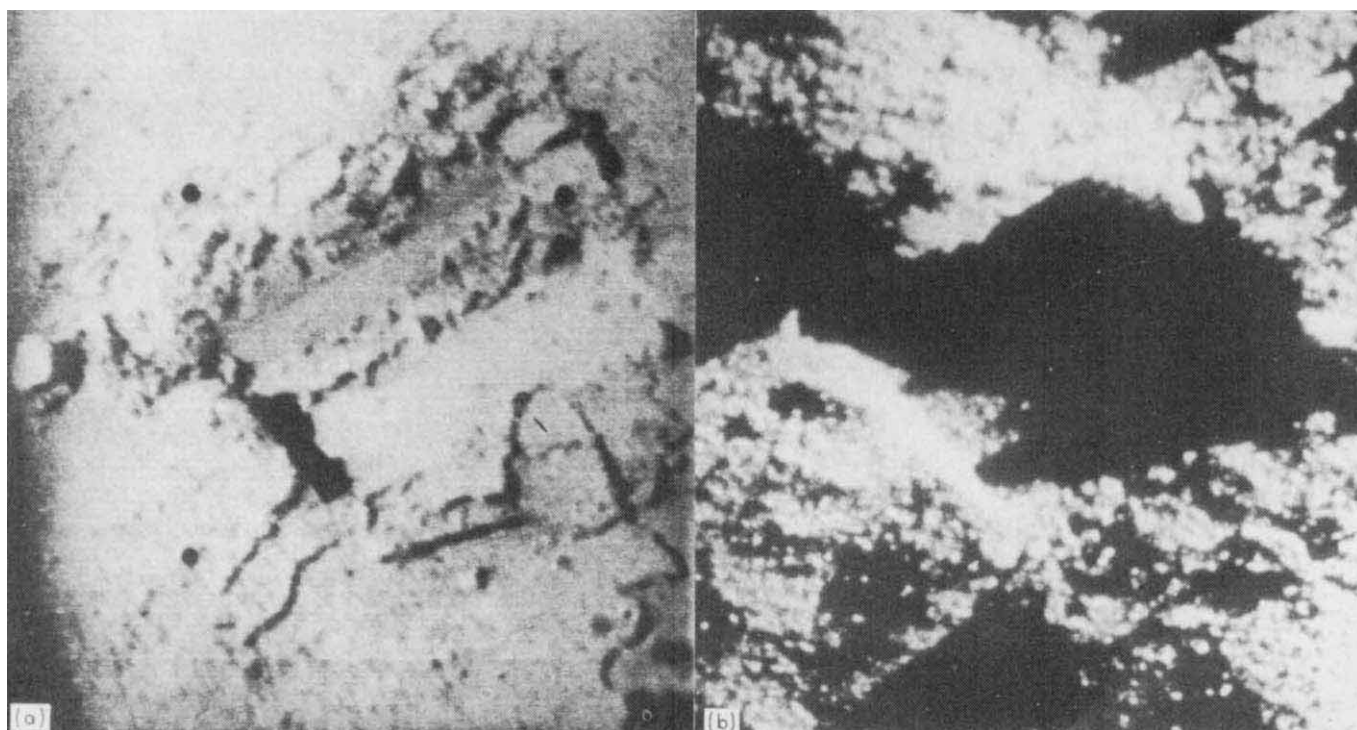


Fig. 2 Lunar surface disturbed by bearing test made with Surveyor 3 soil mechanics surface sampler (bearing test No. 5). *a*, Portion of picture made with Surveyor 3 television camera on April 30, 1967, at 15 : 39 : 30 UT. View taken from south. *b*, Portion of photograph made with Apollo 12 hand-held camera on November 20, 1969, about 06 : 35 UT. View from north, rotated to match. (From NASA photograph AS 12-48-7126.)



Fig. 3 Lunar surface disturbed by pressure from hood of Apollo 11 closeup camera. Illuminated by flashbulb. *a* and *b* form a stereopair. (NASA photograph AS 11-45-6702-1.)

and, indeed, they warned against this interpretation³⁻⁵. Nevertheless, photographs made by the Apollo 12 astronauts of the areas disturbed by Surveyor 3 help to clarify the matter.

Figs. 1*b* and 2*b* are portions of Apollo 12 photographs showing the same bearing test imprints as Figs. 1*a* and 2*a*. The appearance of the areas inboard (toward the Surveyor) is quite different: rather than a pattern of cracks in an apparently flat surface, these Apollo pictures suggest an irregular surface made up of clods or fragments. The difference in appearance arises from differences in lighting angle. The pictures in Figs. 1*a* and 2*a* were made at Sun angles of 80° and 40°, respectively, above the horizon to the west. Those in Figs. 1*b* and 2*b* were taken with the Sun 23° above the eastern horizon. The 13° slope of the crater wall on which Surveyor 3 rests makes the Sun angles to the surface about 87°, 53°, 10°, and 10°, respectively. The "flat" appearance of Figs. 1*a* and 2*a* is a result of the high Sun angle; the low angle lighting of Figs. 1*b* and 2*b* shows the topography better. The high angle lighting is useful, however, in showing the existence and extent of the pattern along which the soil broke into the clods evident at low Sun³.

Fig. 1*c* was taken a few seconds after Fig. 1*b*, from a slightly different angle. The two figures form a stereopair. Viewed stereoscopically, they show clearly the three-dimensional character of the disturbed material; instead of flat "tiles", one sees a pile of roughly equiaxed clods.

The Apollo closeup pictures, such as Fig. 3*a*, were taken with artificial illumination at high angle above the horizontal⁴; no comparable pictures of the same areas were made with low lighting. Fig. 3*b* forms a stereopair with Fig. 3*a*; stereoviewing of the pair reveals strong vertical displacements across the "cracks". At normal stereoviewing separation angles the vertical displacements seem greater than the horizontal size of the blocks. This exaggeration effect arises from the high stereo-separation angle of the camera used⁴; the blocks are probably nearly equiaxed. The impression of flat "tiles" and "crusting", obtained by monoscopic viewing, is an illusion. Rather, the lunar soil deforms and cracks in the same manner as homogeneous isotropic terrestrial soils of moderate bulk density, having a small amount of cohesion (see refs. 1-4).

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Late Quaternary Lake Levels in the Rift Valley of Southern Ethiopia and Elsewhere in Tropical Africa

DURING the past 10 yr information has accumulated pointing to a late Pleistocene/early Holocene lacustrine period in East Africa and the Sudan Zone. On a visit to Ethiopia in January and February 1970 we made a reconnaissance study of the evidence for high lake levels of about this age in the rift valley south of Addis Ababa.

The clearest evidence of the lakes having stood higher than now is in the region of four lakes between 100 and 200 km from Addis Ababa. Lakes Ziway at about 1,652 m and Langano at about 1,590 m drain into Abiyata, 1,582 m, which in recent decades has overflowed from time to time into Shala, 1,567 m. Traces of old strand lines can easily be distinguished from the air near all the lakes and notably over an area of about 150 km² north of Lake Abiyata (Fig. 1).

At the beginning of this century travellers in the area reported finding sub-fossil Mollusca high above the present lake levels¹. Nilsson recognized² several well developed, horizontal beaches at different levels, the most important being a terrace situated 40 m above Ziway which he placed at 119 m above Shala. (Reliable altitudinal control is not available at present and use is made of aneroid barometer readings which may be in error by some metres.) At the 119 m level, Nilsson concluded, the four Galla lakes were joined together to form a single large lake that overflowed north into the Awash valley (Fig. 2), Mohr agreed³ with this conclusion and

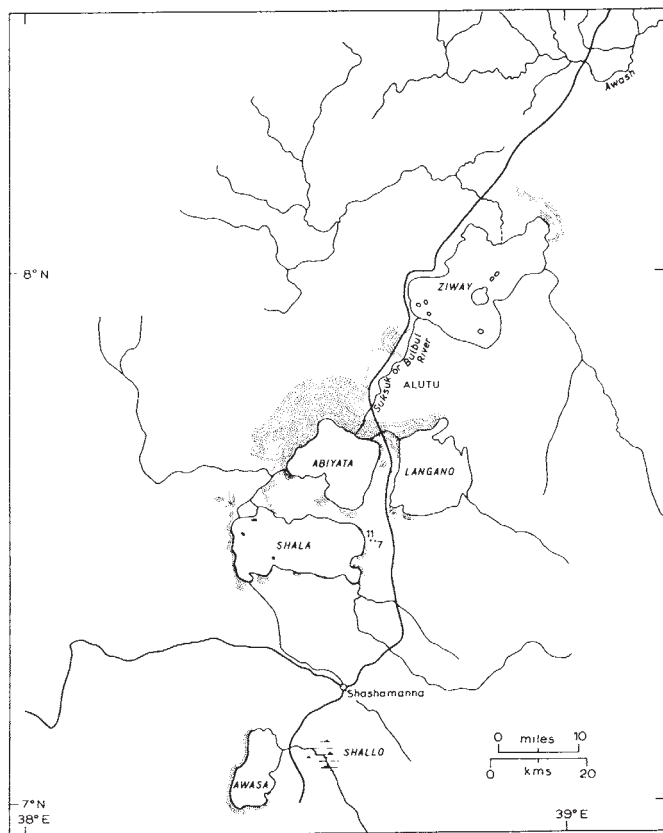


Fig. 1 The Galla lakes.

mentioned lake terraces at several levels. He noted that not all of them are developed around every lake, nor are the lowest and latest terraces always interconnected between the present-day lake basins.

The area, lying as it does within the rift, is unstable but there is no clear evidence that the old strand lines have been displaced to any extent by faulting or tilting. The strand lines seem to mark the levels reached by lakes which formed after transverse movements that separated the rift into several more or less independent, structurally defined basins and disrupted older Quaternary lake deposits⁴. Within and around the basin occupied by the four lakes are several large, dormant volcanoes, some of which have been active in the past few centuries. It seems likely that old strandlines are particularly well developed north of Lake Abiyata because some 30 m or more of pyroclastic grits and gravels accumulated there in the old lake, after being carried by wave action and currents from

the Alutu volcano from which they had either been ejected or had been eroded by gullies in the volcano's slopes. These lake sediments are exposed in the trench cut through them by the Bulbul river flowing from lakes Ziway to Abiyata.

The highest beach material possibly belonging to this lacustrine period consists of rounded cobbles which rest on a rock surface about 3 km west of Lake Ziway and at a height of 130 m above Shala which, as the lowest lake, is used henceforth as datum level. No clear beach formations, however, were found above 116 m. A beach with small fragments of gastropods occurs to the south of Lake Langano at 111 m, and lake limestones, probably formed in association with algae, were found on rocky slopes north-east of Lake Shala at 90–97 m. Several sections of lake sediments, including beds of Mollusca and shelly limestone, were exposed by gullies leading down to Shala, Langano and the Bulbul river, at various heights between 104 and 44 m above Lake Shala.

The Mollusca have been examined by Mr B. W. Sparks (Cambridge University Department of Geography), who has identified several thousand individuals belonging to sixteen species. The assemblages are comparable with those living today in large freshwater lakes in other parts of the African rift valley system. They include large numbers of *Melanoides tuberculata*, *Valvata nilotica*, *Anisus natalensis* and *Pisidium moitessierianum*. Dr P. H. Greenwood (British Museum (Natural History)) has identified a large number of very well preserved small fish bones as being principally *Barbus*, very similar to the *Barbus paludinosus* known today in some, if not all four, of these Galla lakes. A single obsidian microlith was found in beach material 89 m above Shala and 2 km east of that lake.

Samples of about 50 g of *Melanoides tuberculata* from two of the strand line deposits have been radiocarbon dated by Professor Kigoshi (Gakushuin University, Tokyo). The age calculations are based on a half-life of ¹⁴C of 5,570 yr. The results are as follows: GaK 3386, 84 m above Shala (c. 1,651 m A.S.L.) 9,220 ± 190 BP; GaK 3387, 58 m above Shala (c. 1,625 m A.S.L.) 5,610 ± 100 BP.

These results suggest that about 9,240 yr ago the three southern lakes were united and were linked to Ziway which probably stood at about the same level as it does now. About 5,630 yr ago the three lakes were still (or again) united, but at a level 26 m lower.

These dates for high lake levels in southern Ethiopia are similar to those that have been obtained from other parts of the rift valley system and from the southern Sahara and Sudan Zone⁵.

The Songwe river gorge has exposed fluvio-lacustrine beds formed at the margin of Lake Rukwa when it stood at a high level; clam shells in them have been dated to 8,060 ± 120 and oyster shells to 9,740 ± 130 BP⁶. Studies of saline beds, diatoms

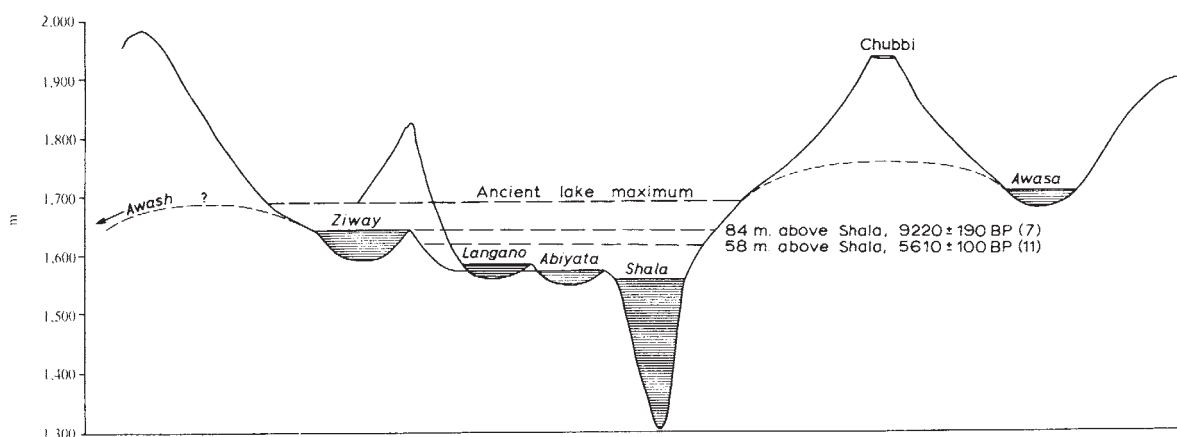


Fig. 2 NE-SW section through the Galla lakes basin.

and fossil pollen grains have shown that for some thousands of years before 12,000 BP, Lake Victoria lacked an outlet and was surrounded by savanna; then the water rose and the vegetation changed to tropical forest⁷. In the Kenya rift, a lake at a height of more than 120 m occupied the Nakuru-Elmenteita basin, about 9,650 ± 250 BP, where the lakes today are little more than large but shallow pools⁸. Between about 12,300 and 8,500 yr ago it seems that lake levels were high and then, after a phase when they dried up, the levels again rose, this time to a level of about 50 m, about 5,000 yr ago. In the Naivasha basin, immediately to the south, a deep lake existed from 9,200 to 5,650 BP and eventually dried out a little over 3,000 yr ago⁹.

To the north, near the Ethiopian frontier, Lake Rudolf started to rise about 13,000 BP and seems to have stood at more than 60 m above its present level until about 5,000 BP¹⁰. In the Omo Valley, north of the lake, flood plain and lakeshore sediments from Member IVa of the Kibish formation have been dated to between 9,700 and 7,700 BP and from member IVb to 5,900 to 5,300 BP. These last sediments standing 80–85 m above the modern lake were laid down when Rudolf still overflowed to the Nile¹¹. At the north-east corner of the lake, at Ileret, a date of 9,360 ± 135 BP has been obtained from the lacustrine (Galana Boi) beds¹². At Lake Stefanie (Chew Bahir), less than 100 km to the north-east of Rudolf, there are lake limestones, almost certainly algal limestones of several different kinds, which contain abundant *Etheria* and some gastropods. They encrust the rocky islands at the south-east corner of the dry lake floor to a height of 20 m above the lake bed¹³. At the other end of the Ethiopian rift, in the Danakil depression of Eritrea, lake sediments have been dated to between 8,940 and 5,600 BP¹³.

Whiteman has recently reviewed¹⁵ the Pleistocene and recent history of the Sudan Republic and Wendorf *et al.* have discussed¹⁶ the late Palaeolithic in Egypt. The sequence of deposition and erosion in the Nile Valley is difficult to interpret climatically. Very long narrow lakes stretched far up the White Nile from Khartoum leaving one terrace at 386 m that can be traced as far south as Melut and another at 382 m as far as Kosti. Shells from the latter have given dates 11,300 ± 400 (in a millenium with exceptionally high floods in upper Egypt) and 8,370 ± 350 BP.

Some of the first clear evidence of a late Pleistocene/early Holocene lacustrine period in tropical Africa came from the plains of Ténéré where Faure, Manguin and Nydal¹⁷ obtained dates chiefly from 9,500 to 7,000 BP for lake deposits in what is now truly arid desert. At about this time Lake Chad was enormously expanded; it occupied an area of some 350,000 km² and overflowed by way of the Mayo Kebbi and the Benue river to the Atlantic. Mega-Chad, as the great lake has been called, may have shrunk about 7,000 BP but it was again a very large lake indeed about 5,400 yr ago¹⁸.

The mountain massifs of Tibesti, Hoggar and Air in the Sahara together with the lake depressions at their margins provide sequences of Quaternary erosion and deposition that have been interpreted climatically. Rivers draining into Mega-Chad from Tibesti built great deltas into the lake between 10,000 and 6,000 BP according to three dates from shells collected from the base and the upper part of the formation¹⁹. A "middle terrace" in the mountains consists of deposits that accumulated between 12,000 and 8,000 BP and from Begour crater, in a very dry area in north-west Tibesti²⁰, a date of 8,295 ± 130 has been obtained from near the top of lake deposited pyroclastics about 3 m thick.

In general there are few high-level lake deposits in tropical Africa with dates between 18,000 and 13,000 BP. Between 13,000 and 7,000 yr ago it is clear that lakes were for long periods if not for the whole time higher and larger than now, when temperatures were probably similar to those of today. Lake levels seem to have been lower for the next thousand years after which they fluctuated through a smaller range. Further work on lake basins such as those in the Ethiopian

rift should throw more light on the details of the sequences of climatic changes involved and the degree to which they were contemporaneous over large regions of the continent.

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Occultation of Beta Scorpii C by Io on May 14, 1971

PHOTOELECTRIC observations of the occultation of the fifth magnitude star β Scorpii C by the satellite Io (Jupiter I) on May 14, 1971, were made in Florida, Jamaica and the Virgin Islands. Some visual observations were also made. This was the first occasion on which accurate observations of such a rare event have been obtained, although several visual observations of the occultation of a star by Ganymede (Jupiter III) were made in 1911. The predictions¹ were only issued a few weeks before the event, and the track of the occultation was then very uncertain owing primarily to the uncertainty in the declination of Jupiter. It has been estimated that Io will occult a star as bright as β Scorpii C only once per millenium on average.

Photoelectric light curves and accurate timings of various portions of the event were obtained as follows: B. A. Smith and S. A. Smith monitored both immersion and emersion in ultraviolet light with a portable 20 cm telescope near Kingston, Jamaica; P. Bartholdi and F. Owen recorded immersion and emersion in blue light with a 40 cm telescope at a hilltop site in St Thomas, Virgin Islands; F. W. Fallon and E. J. Devinney measured immersion in yellow light with their 68 cm telescope near Tampa, Florida; and J. Oliver measured immersion in both blue and orange light with a 75 cm telescope near Gainesville, Florida. Another attempt by B. O'Leary, R. Brinkmann, and C. Slaughter at Guanica, Puerto Rico, was foiled by wind and clouds.

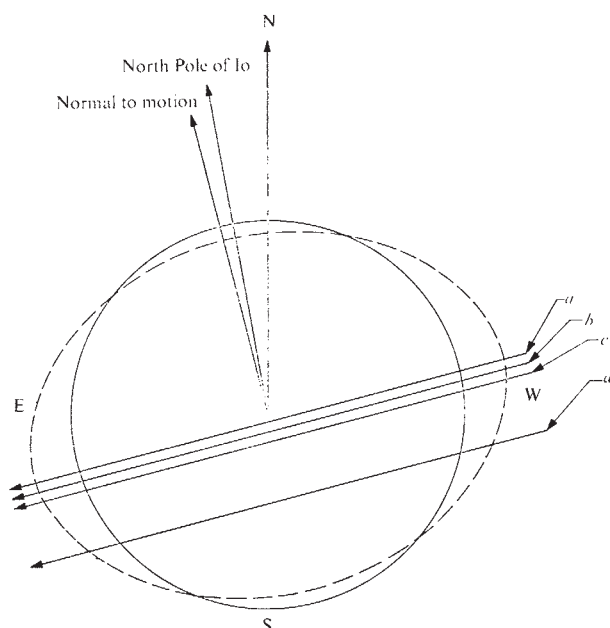


Fig. 1 Circumstances of the occultation of β Scorpii C by Io on May 14, 1971, with theoretical direction of North Pole. The tidal and rotational bulge of Io (greatly exaggerated) is shown as a dashed ellipse. *a*, Gainesville, Florida; *b*, Tampa, Florida; *c*, St Thomas, Virgin Islands; *d*, Kingston, Jamaica.

Fig. 1 shows the apparent path of the star with respect to Io, as seen from each observing site, based on the preliminary analysis of the timing data for four disappearances and two reappearances. If Io is assumed to be spherical, the deduced value of the diameter of Io is $3,659 \pm 5$ km. At this stage in the analysis, the data seem to be insufficient in themselves to allow a determination of the flattening, if any, of the satellite. For a homogeneous fluid body in hydrostatic equilibrium, the equatorial radius should be 20 km greater than the polar radius as seen from Earth at the time of the event, the major cause being permanent tides raised by Jupiter. It is hoped that further refinements in the reductions will yield an observed value for the flattening of Io. If de Sitter's value² for the mass ratio Jupiter/Io is adopted, the density of Io is found to be 2.82 ± 0.23 g cm⁻³. The escape velocity is found to be 2.30 km s⁻¹.

None of the light curves showed any signs of an atmosphere on Io: in all cases the curves were flat just before and after occultation with abrupt changes in intensity at immersion and emersion. The presence of even a tenuous atmosphere would be indicated by a gradual change in intensity during a period of several seconds before and after occultation, caused by the defocusing of differentially refracted starlight through the gaseous medium. The observations showed that the light intensity changed by no more than a few per cent during these phases, leading to an upper limit of $\sim 10^{-4}$ mbar surface pressure for N₂ and CH₄ and $\sim 10^{-3}$ mbar for H₂. Because molecular hydrogen would most likely have escaped from a primordial atmosphere, 10^{-4} mbar is the probable upper limit for any atmosphere on Io.

Additional "events" were noted in some of the light curves. The three best defined such events are all consistent with the hypothesis that the occulted C-component of this known quadruple star system is itself a double star, with the new companion approximately two magnitudes fainter in the blue at position angle $308^\circ.2 \pm 1^\circ.2$, separation $0''.097 \pm 0''.002$.

The high resolution light curves indicated that both the decline and return to normal light were slower than that predicted by diffraction theory. This is interpreted to indicate a finite stellar diameter for the brighter C-component, which is estimated to be $0''.0002$, in good agreement with theoretical expectations.

Further details will be published by the individual authors in the near future.

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Further Evidence for a Black Hole in β Lyrae

DEVINNEY¹ has shown that the observational peculiarities of the binary system β Lyrae can best be understood in terms of the secondary mass being a collapsed star (black hole) surrounded by an opaque or nearly opaque disk. This communication points out that the recently released² ultraviolet photometry from the Orbiting Astronomical Observatory (OAO) leads to the same conclusion. Fig. 1 shows the light curves of β Lyrae given in ref. 2, for which the stated accuracy is ± 0.01 magnitude. One might have some reservations about these observations because the shorter wavelength light curves fail to close after one cycle and the presentation (hand-drawn curves instead of the original observation points) is counter to normal practice. It may, however, be a very long time before confirming observations of this extremely interesting binary can be gathered, and they do relate in an important way to the question of whether β Lyrae contains a collapsed star. Kondo *et al.*² mentioned briefly the possible presence of a black hole in the system, but not for the reason advanced here.

At first glance, the eclipse of the secondary component in visible light appears reasonably deep, but most of the depression at phase 0.5 in the light curve is due to the ellipticity effect, while the actual eclipse accounts for a few hundredths of a magnitude only. The unexpected result shown by the OAO observations is that this eclipse becomes, progressively, very much deeper into the ultraviolet. Indeed, at $1380 \text{ \AA}$, the shortest effective wavelength observed, secondary eclipse is nearly as deep as primary, and the trend strongly suggests that it becomes the deeper eclipse at shorter wavelengths.

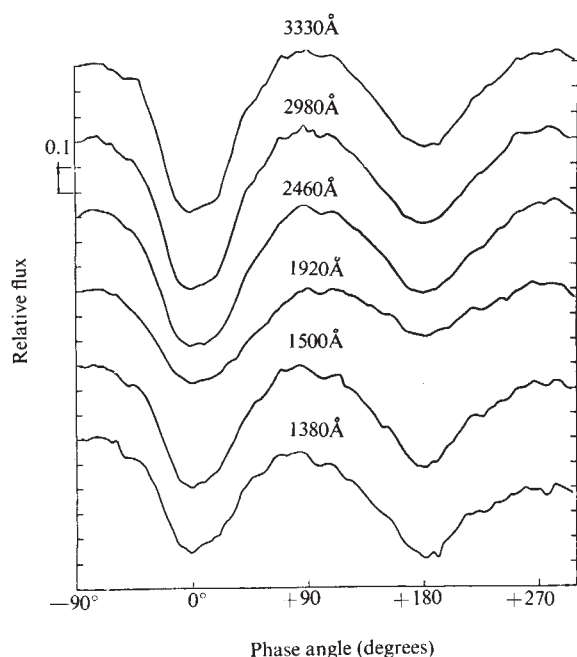


Fig. 1 OAO light curves of β Lyrae given by Kondo, McCluskey, and Houck.

Now one of the most fundamental and elementary principles in the interpretation of eclipsing binary light curves is that the ratio of the depths of the two eclipses is essentially determined by the surface brightness ratio of the two components—here the primary star and the secondary disk (since all recent models of β Lyrae involve a disk or cloud around the secondary star). For a normal binary, the component with greater surface brightness is the one of greater temperature and, because two Planckians for different temperatures are non-intersecting, this component will have the deeper eclipse at all wavelengths. For β Lyrae, however, the depth ratio changes strongly with wavelength in the opposite sense to that expected for Planckian sources, such that the roles of the primary and secondary eclipses are probably reversed shortward of, say, 1200 Å. The necessary conclusion is that the secondary continuum radiation is very strongly non-Planckian, at least insofar as its absolute intensity is concerned. That is, the light of the secondary component is unquestionably very “blue” as shown by the run of the primary and secondary depths with wavelength, and this is indicative of high temperature radiation. But it does not have the intensity (that is, surface brightness) of high temperature radiation because the secondary eclipse is a great deal shallower than primary eclipse at visible wavelengths. The secondary shines therefore by dilute high temperature radiation.

This could describe thermal bremsstrahlung from a very hot, optically thin gas, but we cannot picture this as being generated directly from the entire secondary object since the fact that the secondary causes eclipses means that it cannot be optically thin. Furthermore, its temperature would have to be very high (say 10^6 K or greater) and there is no reasonable mechanism for maintaining such a temperature. Of course, we cannot be dealing with a hot star surrounded by a cloud of intermediate optical thickness because a star as massive as is required by the spectroscopic mass function would heat the cloud to quite a high temperature and thus render it readily visible. In fact the cloud could not even exist in the radiation field of such a star for any appreciable time—the chief argument by Kondo *et al.*² in mentioning the black hole possibility. Thus, we are forced to a centrally localized source of high temperature continuum radiation and very modest luminosity. So far as the present evidence shows, the source itself may be either optically thin or optically thick, but in either case only a small percentage of its light can reach us directly and the

exterior of the disk must shine by this light after it has undergone (typically) several scatterings.

These features of the secondary energy source—very “blue” spectral energy distribution, spatial concentration in the centre of a cloud or disk of material, and much lower luminosity than we expect for a star of the indicated mass—strongly suggest that accretion of matter by a highly condensed mass is responsible (see, for example, refs. 3, 4). Because the mass we require is of the order of $20 M_{\odot}$, there remains only one candidate—a star which has collapsed to its gravitational radius.

I thank Dr George E. McCluskey for the light curves of β Lyrae.

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Release of Carbon Dioxide from Frozen Soil to the Arctic Atmosphere

DELINEATION of sources and sinks of CO_2 is fundamental to understanding carbon cycling in an Arctic ecosystem. Kelley *et al.*¹ observed a large, variable increase in CO_2 concentration at the tundra surface over ambient air CO_2 beginning a few days after the first snowfall. This increase continued into December, at which time CO_2 declined to relatively stable concentrations approaching ambient air levels. CO_2 at the surface increased from early May to late June until the snow disappeared. Bashenina² also observed CO_2 concentrations under the snow higher than atmospheric values. The present investigation was undertaken to explain the source of the subnivean CO_2 .

Soil cores, 2.5 cm in diameter, were collected from five sites in northern Alaska during September 17–20, 1970. The cores included organic and mineral material extending from the tundra surface to the level of permanently frozen ground. Core length averaged 24 cm ranging from 17 to 31 cm. The cores were sealed, weighed, and stored at 4° – 10° C until subjected to laboratory analysis.

The cores were weighed at the time of analysis to verify that water loss during storage was less than 1%. They were then cooled to freezing temperatures during which CO_2 was monitored by infrared gas analysis. This was accomplished by placing the cores in a 2.5 cm diameter cylindrical ‘Pyrex’ chamber with ball and socket joints to accommodate air intake and outlet, and a thermocouple to monitor core temperature during analysis. An ascarite cell in the intake line provided CO_2 free air to the core. CO_2 detected by the analyser in the outflowing air stream was concluded to be of core origin.

A series of accurately controlled CO_2 reference gases was used to calibrate the analyser. CO_2 from the cores and temperature were recorded simultaneously on a two-channel strip chart recorder. Total water content and pH were determined for each core subsequent to freezing.

The section of the CO_2 curve of particular interest in this investigation (Fig. 1) corresponds to the period of phase change of the soil moisture. An important assumption was made that the evolved CO_2 , represented by the area under the curve in Fig. 1, above the dashed line, must be due to freezing of the core. A biological source is ruled out or diminished in importance in that biochemical reaction rates normally vary directly with temperature. Since core temperatures were held

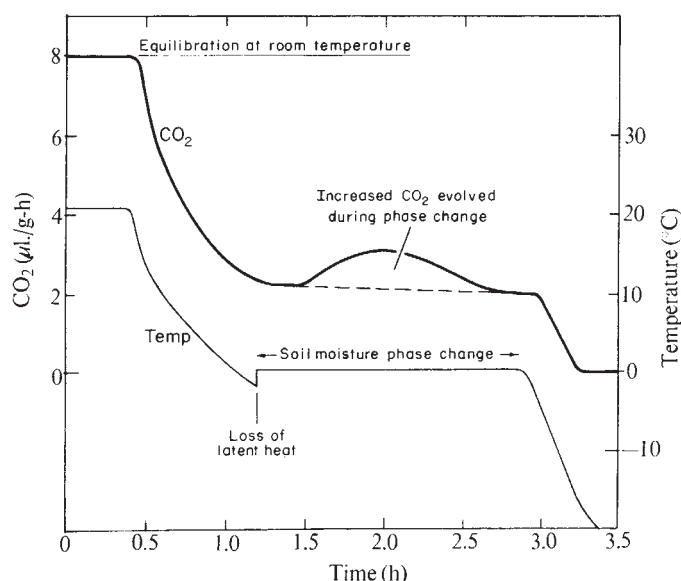


Fig. 1 Evolution of CO₂ relative to temperature from a freezing tundra soil core.

constant at 0° C during phase change, CO₂ production from biological sources would be expected to remain constant or perhaps be inhibited by solidification of the soil water.

The results of the analyses are shown in Table 1. Assuming the lowest CO₂ quantity (0.1 μl./g) observed reflects the natural system and is constant over the tundra surface, approximately 500 l./Ha would be released from the surface 30 cm by the freezing process. A corresponding release for the highest observed value (2.0 μl./g) would be 90,000 l./Ha. The CO₂ thus released from solution apparently escapes to the atmosphere at varying rates throughout the period when soils are frozen. Greatest rates of escape occur in the autumn and spring¹.

During the summer, decomposition within the active layer of tundra results in a soil saturated with CO₂ (ref. 3). As the soil freezes, CO₂ should be evolved. Unlike the trapped gas that appears in the centre of an ice cube when a volume of water

is frozen, a soil core represents a different situation. The presence of plant roots, organic matter, and soil particles allows many routes for entrained gas to escape.

The "ice cube" effect was apparently observed when autoclaved bentonite saturated with CO₂ enriched water was rolled into cores and subjected to the same freezing treatment as the soil cores. No increase in evolution of CO₂ occurred on freezing. The possibility that a high proportion of the CO₂ remained dissolved in unfrozen, interfacial water in the clay core cannot be discounted, however⁴.

Cores that provided the highest evolution of CO₂ were characterized by coarse texture and high moisture content. Cores collected from a sandy bluff along the Meade River 100 km south of Barrow were relatively dry and showed no increase in CO₂ evolution on freezing (not included in Table 1). Cores from a beach ridge near Barrow which contained much gravel mixed with silt and clay size particles and with 5 to 15% higher moisture content than the Meade River cores had detectable CO₂ evolution.

The cores in this investigation were frozen from the surface to the centre. The tundra, however, freezes bidirectionally. Sub-freezing temperatures at the soil surface and at the upper surface of the permanently frozen ground give rise to two freezing fronts. As these two fronts approach each other in the autumn, CO₂ is evolved into the unfrozen layer. Some of the CO₂ may escape to the tundra surface in proportion to texture, cracking, and other avenues of escape producing a highly variable autumn rise in CO₂ concentration as observed by Kelley *et al.*¹. Some CO₂ may become trapped within the freezing active layer and may slowly escape causing a soil surface CO₂ level slightly higher than ambient air during the winter months.

Associated with the increase in tundra surface temperatures in the spring is an increase in the subnivean and ambient concentrations of CO₂. Further release of trapped gas as a result of differential warming of the soil may be the source of the spring rise reported by Kelley *et al.*¹. Amplification of this spring rise by biological systems cannot be ruled out once minimal conditions for growth and assimilation are met.

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Table 1 Carbon Dioxide Concentrations evolved from Freezing Tundra Soil Cores

Habitat	CO ₂ μl./g dry soil	pH	Moisture content % wt
Umiat—Colville River floodplain	1.5	4.4	97.4
	1.0	4.9	77.9
	0.8	4.5	89.1
	0.5	4.7	92.9
	0.9	4.6	116.0
	1.2	4.9	83.3
	0.7	4.7	62.7
	0.9	4.9	66.5
	2.0	5.1	67.4
Barrow—wet sedge meadow	0.4	3.7	57.5
	0.3	3.7	76.4
	0.1	3.8	46.8
	0.1	3.7	54.9
	0.7	3.9	109.1
	0.6	4.1	63.8
Barrow—marsh	0.1	4.5	44.3
	0.2	5.1	40.9
	0.2	5.1	46.1
	0.1	5.1	44.8
	0.1	4.8	53.3
Barrow—raised beach ridge	0.1	4.3	30.1
	0.1	4.3	36.6
	0.7*	5.2	51.6
Barrow—raised beach ridge	0.1	5.2	33.8
	0.8	5.2	34.5
	0.2	5.0	38.9

* Data for this core are graphed in Fig. 1.

BIOLOGICAL SCIENCES

Actin in Sperm Tails and Meiotic Spindles

In many cases cellular motility seems to be due to interactions between actin and myosin¹⁻⁸. Actin (or actin-like material) has also been identified in other cellular systems which exhibit motility⁹⁻¹⁴ and actin-like and myosin-like proteins have been claimed to be isolated from mitochondria¹⁵ and chloroplasts¹⁶. While it is not proved that motility in these systems is due to

actin and myosin, actin-myosin interactions are probably involved. Flagellar (ciliary) motions and chromosome movements, on the other hand, have generally been attributed to microtubules¹⁷⁻¹⁹, and thus there seemed to be two different kinds of motile systems; one based on actin-myosin interactions and the other on microtubules. We have found, however, actin-like filaments in both sperm tails (flagellae) and meiotic spindles of crane flies. Although we are well aware that we have demonstrated merely the presence of actin and have by no means proven that the flagellar and spindle actin has anything to do with motility, we nonetheless suggest that motility in all motile systems in higher cells is based on actin-myosin interactions.

We glycerinated crane fly testes (*Nephrotoma suturalis* Loew) in a 1 to 1 mixture of pure glycerol and standard salt solution¹¹. All the cells in any one testis are in roughly the same stage of maturation, and in different experiments we used testes with cells in division, or with spermatids, or with mature sperm. After 3 days glycerination, the cells were removed from the testes and processed for electron microscopy, either for negative staining with 1% uranyl acetate²⁰ or for embedding and sectioning. For negative staining, the cells were first ruptured in standard salts solution; some aliquots were incubated with heavy meromyosin (HMM)²¹ before negative staining, other aliquots were incubated with HMM and ATP, whilst other aliquots were negatively stained directly. For embedding and sectioning, glycerinated cells were incubated for 24 h with HMM, and then fixed with 2% glutaraldehyde, postfixed with 1% osmium tetroxide, and processed using standard techniques²⁰.

Actin was prominent in negatively stained preparations of spermatids and mature sperm. The actin was identified as such by its characteristic appearance and dimensions²¹, and by the facts that it bound HMM to form characteristic arrowheads²¹ and that ATP inhibited arrowhead formation²¹. The individual actin filaments were about 50 Å in diameter but very often were packed into bundles which were up to around 800 Å wide and which were several microns long (Fig. 1a). There were as many as fifteen to twenty filaments per bundle. In any one bundle the actin filaments were often of opposite polarities, that is the HMM arrowheads on adjacent actin filaments often pointed in opposite directions (Fig. 1b). These actin-containing bundles of filaments are distinguishable from axoneme microtubules morphologically and by the absence of HMM binding to microtubules.

We examined by electron microscopy sections of one cell in anaphase and several metaphase cells, the stages having been determined by light microscopy. We saw some HMM-reacting filaments in the spindle areas. These actin-like filaments had the characteristic appearance of "fluffy" filaments after HMM-binding^{10,11}. Some of the actin was near chromosomes, oriented in the pole-to-pole direction, and in some sections a few filaments might have been attached to the poleward side of some chromosomes. There was also actin near the spindle poles and at the cell periphery.

Although we cannot prove that actin from sperm or spindle is involved in sperm or chromosome motion, it would be surprising if this were not so. The presence of actin in other motile systems, together with the identification of actin in sperm tails and spindles, strongly suggests that actin-myosin interactions are responsible for all kinds of motility in higher cells.

Our identification of actin in sperm tails confirms earlier biochemical indications that sperm tails contain actin-like and myosin-like components which react with muscle myosin and actin, respectively^{22,23}, and that a myosin-like component in cilia reacts with muscle actin^{24,25}. The identification of actin in spindles confirms earlier evidence from isolated sea urchin mitotic apparatus. Aronson²⁶ found that fluorescent-labelled HMM binds to isolated mitotic apparatuses, and Miki-Noumura²⁷ found a 2.3S component of isolated mitotic apparatus that was like actin in that its viscosity increased when it was transferred from KI solution to one with ATP.

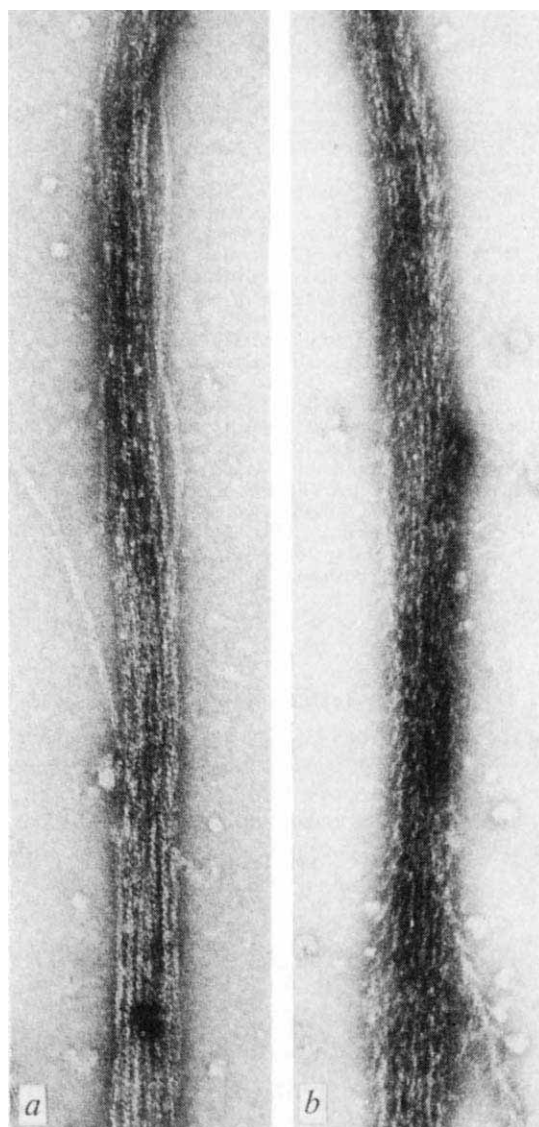


Fig. 1 *a*, Negatively stained preparation of bundle of actin filaments from mature *Nephrotoma* sperm ($\times 131,000$). *b*, Bundle of actin filaments from mature *Nephrotoma* sperm reacted with HMM. The opposite polarity of two of the filaments can be seen ($\times 113,000$).

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Actin in the Mitotic Spindle

I PREVIOUSLY suggested that the shape of the metaphase spindle cannot be maintained if there is tension in the component microtubules¹. Spindle tension has been detected^{2,3} and could be due to some other component pulling the chromosomes over the rigid microtubular framework.

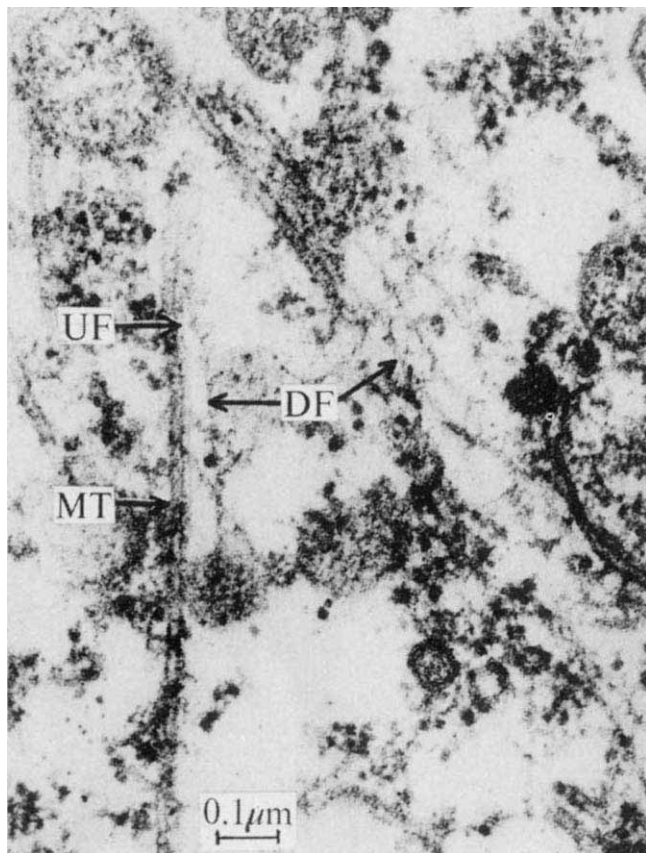


Fig. 1 Part of a metaphase mitotic spindle, long axis of spindle running from top left to bottom right of picture. Oriented, decorated filaments (DF) are shown, and an undecorated filament (UF) associated with a microtubule (MT) ($\times 108,500$).

Aronson⁴ established that fluorescein-labelled heavy meromyosin (HMM) binds to isolated sea-urchin spindles as well as to muscle fibrils, indicating that actin is present in both. I have now located the actin in electron micrographs with the method used by Ishikawa *et al.*⁵.

Locust testis tissue was treated for 24 h at room temperature with 50% glycerol in a buffer containing 0.1 M KCl, 0.006 M phosphate, and 0.005 M $MgCl_2$. The testis follicle wall was torn slightly with a glass needle and the tissue was incubated for a further 24 h with rabbit HMM in a similar buffer at 4°C. The tissue was fixed in 2.5% glutaraldehyde treated with 1% osmium tetroxide, and embedded in araldite. Sections were stained with uranyl acetate and lead citrate.

Mitotic cells of the testis were studied because their spindle microtubules survive glycerination and incubation, whereas spindle microtubules in meiotic cells do not. Three types of filament, in addition to microtubules, can be seen in metaphase mitotic cells. One type runs parallel at a distance of 100 Å to an associated microtubule but there are no apparent cross links (Fig. 1). This type of filament is never associated with heavy meromyosin. Another type forms a complex with HMM, which characterizes the filament as actin. Most of these filaments lie parallel to the long axis of the spindle but are not closely associated with any microtubules. The third type of filament is found at the periphery of the cell, parallel to the surface, and always forms a complex with HMM. It is found in all testis cells, whether in division or not.

Although actin has only been shown to be present in the spindle, it is probably involved in the movement of chromosomes in which case chromosome movement would involve, like many other cell movements^{6,7}, an interaction between actin and myosin. The observations suggest that either the microtubules themselves have myosin-like properties or they are associated with myosin which is lost during preparation of the tissue.

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Protein Polymorphism

In their well known study of protein polymorphism in *Drosophila pseudoobscura*, Prakash, Lewontin and Hubby¹ showed that most loci reveal little or no differentiation in allele frequencies in different sub-populations; they concluded that the observed polymorphisms cannot be due to random genetic drift of neutral mutations and are most likely to be caused by some form of balancing selection. This conclusion has been challenged by Kimura and Ohta² on the grounds that only a small amount of migration between the sub-populations is required to make them into an effectively single panmictic population in which one would not expect to find much local differentiation in allele frequencies under the neutral mutation theory originally proposed by Kimura³. The purpose of this letter is to point out another feature of the data of Prakash

*et al.*¹ which suggests that the polymorphic alleles are not selectively neutral.

Table 1 shows in a simplified form the results of Prakash *et al.*¹ for loci with three or more alleles. (The esterase-5 locus is excluded because it is clearly different from the rest, no fewer than twelve alleles having been identified; the data for the isolated population around Bogota are also excluded since this population is much less variable, probably on account of genetic drift.) The alleles are given in the order of electrophoretic mobility, and have been classified arbitrarily into rare alleles (with a frequency less than 10%) and common alleles (with a frequency greater than 10%). There is a marked tendency for the rare alleles to occur at the beginning or the end of a sequence and for the common alleles to occur in the middle of a sequence; for example, when there are two rare alleles and one common allele the sequence is always RCR and never CRR or RRC. If these alleles are selectively neutral one would expect all possible orders of the sequences to be equally likely; on the other hand, this kind of result would be expected if there is an optimal genotype, which may be heterozygous or homozygous, and if the difference in electrophoretic mobility of two alleles can be regarded as a crude measure of their functional difference.

Table 1 Data of Prakash *et al.*¹ on Polymorphism in *Drosophila pseudo-obscura*

		Strawberry canyon					Mesa Verde					Austin					Probability of observed type of sequence in most polymorphic population
Population	Locus	Allele					Allele					Allele					
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
Pt-7		R	R	C	R		-	R	C	R		-	R	C	R		$\frac{1}{3}$
Leucine aminopeptidase		R	R	C	R	-	R	R	C	R	-	R	R	C	R	R	$\frac{1}{3}$
Pt-8		R	C	C	-		R	C	C	R		R	C	C	R		$\frac{1}{3}$
Xanthine dehydrogenase		R	R	C	C	R	R	R	C	C	R	R	R	C	C	R	$\frac{1}{3}$
Larval acid phosphatase		-	C	-			-	C	-			R	C	R			$\frac{1}{3}$
Acetylaldehyde oxidase-2		R	R	C	R		-	-	C	-		-	-	C	-		$\frac{1}{3}$
Octanol dehydrogenase-1		-	C	R			R	C	R			-	C	-			$\frac{1}{3}$
Pt-10		R	C	C			R	C	R			R	C	R			$\frac{2}{3}$
α -Amylase-1		R	C	C			-	C	C			-	C	C			$\frac{2}{3}$

R, rare (frequency <0.1); C, common (frequency >0.1); -, not present in this population; blank, no such allele present in any population.

To test this hypothesis the probability of each type of sequence was calculated on the assumption that all arrangements are equally likely; for example, the probability of RCR is one-third because there are three arrangements of which only one has C in the middle, the probability of RCCR is one-sixth since there are six arrangements of which only one has two Cs in the middle, and the probability of RCC is two-thirds since there are three arrangements of which two have an R at the end. Because of the high correlation of the allele frequencies in the different populations, it would clearly be wrong to count all the sequences as independent observations. For each locus the sequence from the most polymorphic population was therefore used, and the probability of the type of sequence in this population is shown in the last column of Table 1. Because each observed sequence was of the most extreme type, it is possible to obtain an overall significance level by multiplying these probabilities together. This procedure gives a probability of 1/12,150.

It can be concluded that each type of sequence is not equally likely. This finding is incompatible with the theory, advanced by Kimura³ and Kimura and Ohta², that protein polymorphism is due to random genetic drift among a large number of neutral isoalleles in a finite population of fairly constant size. The most plausible alternative theory is that the alleles involved are not selectively neutral.

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Ultrafiltration in the Gastropod Heart

It is generally agreed that the urine of most molluscs is produced initially by ultrafiltration of the haemolymph into the pericardial cavity, and that the composition of this initial filtrate is modified by the kidney before being expelled as urine¹⁻⁷. The only exceptions are the terrestrial pulmonate gastropods, in which urine seems to be filtered directly into the kidney^{8,9}. Pierce¹⁰, however, is not convinced that the heart is the filtration site in lamellibranchs, and suggestions that ultrafiltration occurs through the wall of the auricle in most gastropods were not substantiated by ultrastructural studies of terrestrial and freshwater pulmonates¹¹.

Using the snails *Potera lineata* and *P. varians* (Gastropoda, Prosobranchia, Cyclophoridae) collected from forest leaf litter in Jamaica we have shown that urine is initially produced by filtration into the pericardial cavity; electron microscopy has suggested that the ventricle, not the auricle, is the main site of filtration.

Although few figures are available, the similarity between the composition of the haemolymph and that of pericardial fluid (Table 1) suggests the origin of the latter by filtration. This was demonstrated by injecting ¹⁴C-inulin, dissolved in *Potera* Ringer solution, into the rectal sinus of *P. varians*, and removing samples of about 2 μ l. at intervals from the efferent pulmonary vein (leading directly into the auricle) and pericardial cavity. The concentration of inulin in the pericardial fluid rose rapidly to a value slightly higher than that in the haemolymph, and remained so for a range of 2,000-200 c.p.m./ μ l. (Fig. 1). Presumably this slight difference is main-

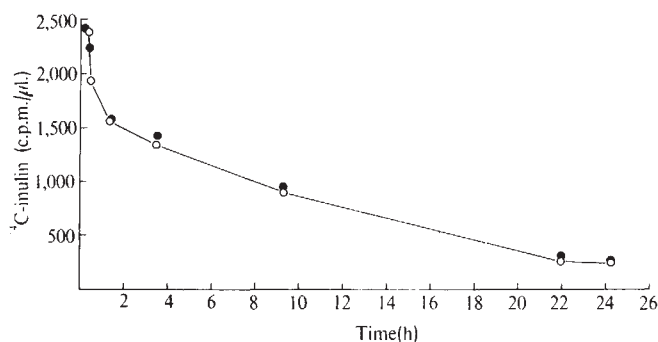


Fig. 1 The concentrations of inulin in haemolymph (open circles) and pericardial fluid (closed circles) of *P. varians* following injection of ¹⁴C-inulin into the rectal sinus at time zero.

Table 1 Comparison between the Composition of Haemolymph and that of Pericardial Fluid in *Potera lineata*

	Osmotic pressure mmol/l. NaCl	Na mmol/l.	Ca mmol/l.	Mg mmol/l.	Cl mmol/l.
Haemolymph	40.8 ± 1.13 (9)	31.4 ± 0.80 (9)	5.1 ± 1.04 (9)	1.5 ± 0.34 (9)	25.1 ± 0.85 (9)
Pericardial fluid	40.7 ± 0.35 (3)	32.0 (1)	3.9 (2)	1.4 (2)	23.0 ± 2.13 (3)

Values are given as mean ± s.e. (number of observations).

tained because it takes a certain time for the fluid to be filtered: fluid present in the pericardial cavity at any one time was filtered from the haemolymph when the latter had a slightly higher concentration of inulin. These results suggest that haemolymph is filtered through the heart into the pericardial cavity. The situation is similar to that in the aquatic proso-branch *Viviparus*.

The outer surface of the auricle is lined by a discontinuous squamous epithelium of seemingly inactive cells with dense cytoplasm and interdigitating branches, but over the ventricle this is replaced by cells (Fig. 2, po) which resemble the podocytes of the mammalian glomerulus¹², and the coelomic sac of the crayfish *Cambarus*¹³, both of which are thought to be concerned with ultrafiltration. Active and senescent cells can be distinguished (Fig. 2). The wall of the ventricle is devoid of an endothelium and its network of muscle fibres is embedded in connective tissue permeated by numerous channels extending from the central lumen to the basal lamina of the epithelium. At the distal ends of the channels the lamina is the only barrier between the haemolymph and the epithelium and these are taken to be the filtration sites (f.s.).

The epithelial cells are raised above the basal lamina by stilt-like processes of the cytoplasm (pr), creating subcellular spaces (sp), which presumably receive the filtrate and open into the pericardial cavity through narrow intercellular channels. Their cytoplasmic processes give rise to fine branches (pe), similar to pedicels, which interdigitate with those of neighbouring cells.

Apart from the absence of a fenestrated endothelium the arrangement is similar to that in the glomerulus, suggesting that in *Potera* ultrafiltration occurs in the ventricle rather than

in the auricle. Since the hydrostatic pressure of the haemolymph presumably reaches its maximum in the ventricle, this would also suggest that it is the more likely site.

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Immunoelectron Microscopic Studies of Type C Virus Particles in ESP-1 and HEK-1-HRLV Cell Lines

A MONOLAYER cell culture (ESP-1) established with cells from pleural effusion of a patient with Burkitt lymphoma (American type) continuously produced virus particles morphologically similar to murine type C virus particles¹. Earlier results¹ of immunodiffusion tests suggest that the type C virus particles in the ESP-1 culture do not seem to have the group specific (gs-1) antigen of the known animal leukaemia viruses. These immunodiffusion tests also did not show the gs-3 antigen common to the viruses of leukaemia of mouse, hamster, rat, and cat.

We now describe studies carried out by the indirect immunoferritin labelling technique^{2,3} on the type C virus particles of the ESP-1 cell line. The extreme sensitivity of the immunoferritin technique in specific labelling of individual virus particles⁴⁻⁶ provides a valuable tool for study of morphological and immunological properties of virus particles in the ESP-1 cell line. Type C virus particles in the human embryo kidney cell culture infected with the murine Rauscher leukaemia virus (HEK-1-HRLV) were used for comparison.

Antisera to MuLV gs and type-specific antigens were obtained from adult (W/FU × BN)F₁ rats with growing transplants of a leukaemia induced in an inbred W/FU rat by wild type Gross virus⁷. By immunodiffusion and immunofluorescence tests, these antisera contained gs-1 but lacked gs-3 antibody⁷. Monospecific antibody to the gs-3 antigen was



Fig. 2 Electron micrograph of the epithelium and part of the wall of the ventricle of *P. lineata*. An active podocyte is shown on the left, a senescent one on the right.

made by immunizing rats with the antigen-antibody precipitin band made by using antisera selected for their reaction to feline leukaemia virus antigen (the gs-3 being represented as the antigen in the anti-gs-3-gs-3 complex). The band was cut from the agar and washed with saline before immunization of the rats. The resulting antiserum contained antibodies monospecific for the gs-3 antigen. The reagents were shown to be monospecific by immunodiffusion test (carried out by G. Geering) and by immunofluorescence test (carried out by Dr J. Hilgers). (Both antisera were supplied by Drs Lloyd J. Old and Gayla Geering.)

Experiments carried out to determine the dilution of serum most satisfactory for use in ferritin labelling showed that dilutions lower than 1:20 produced much non-specific labelling⁶.

The virus particles in the ESP-1 cell culture were not labelled with ferritin by the rat anti-MuLV (gs-1) serum followed by treatment with ferritin conjugated goat anti-rat IgG (Table 1 and Fig. 1a). Virus particles in the HEK-1-HRLV cell line were strongly labelled by the same treatment (Fig. 1b). Although gs-1 antigens are considered internal viral antigens, this test clearly shows that the virus particles are labelled on the viral envelope. Similar labelling was also observed on the viral envelopes of other murine leukaemia virus treated with the same antiserum: type C virus particles in the cells of SJL/J/Cr spleen culture, in induced BALB/c/Dm strain mouse mammary tumour, in spontaneous RIII/Dm strain mouse mammary tumour (D-W) cell line producing A, B, and C particles^{6,8}. Type B virus particles in a (C57 × Af)F1 spontaneous mammary tumour cell line and in the spontaneous RIII/Dm strain mouse mammary tumour culture (D-W) were not labelled with the anti-gs-1 serum⁶.

The results of these tests indicate that the gs-1 antigen of the type C virus particles found in the ESP-1 human cell culture differs from the gs-1 antigen of the Rauscher murine leukaemia type C virus particles adapted to the human embryo cell line and from that of other murine type C viruses tested. These tests were repeated and resulted in identical findings⁹.

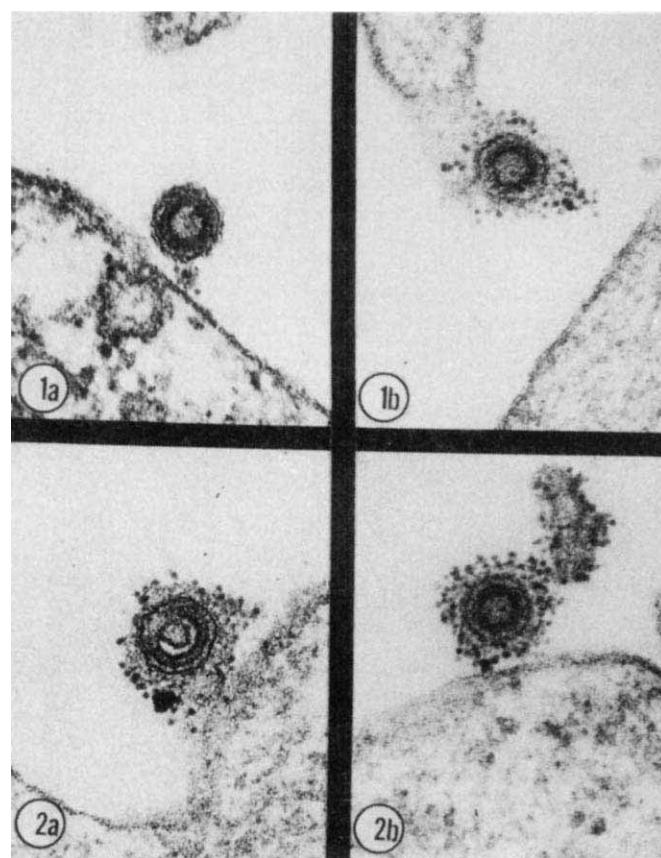


Fig. 1 *a*, Thin section of ESP-1 tissue culture treated with rat anti-MuLV (gs-1) serum followed by ferritin conjugated goat anti-rat IgG. No labelling of type C virus particle ($\times 90,000$). *b*, Thin section of human embryo kidney tissue culture infected with Rauscher murine leukaemia virus (HEK-1-HRLV). Same treatment as *a*. Labelling of type C particle ($\times 90,000$).

Fig. 2 *a*, ESP-1 tissue culture treated with rat anti-MuLV (gs-3) serum followed by ferritin conjugated goat anti-rat IgG. Ferritin labelling of type C particle ($\times 90,000$). *b*, HEK-1-HRLV tissue culture, same treatment as in *a*. Ferritin labelling of type C particle ($\times 90,000$).

Table 1 Results of Immunoferritin Tests on Type C Virus Particles in the ESP-1 and HEK-1-HRLV Cell Cultures

Sera used	ESP-1	HEK-1-HRLV
(a) Rat anti-MuLV (gs-1) untreated, diluted 1:20 and 1:64	—	+
(b) Rat anti-MuLV (gs-3) untreated, diluted 1:20 and 1:64	+	+
(c) As (b) and absorbed with guinea-pig kidney powder and sheep red blood cells, diluted 1:64	+	NT
(d) As (b) and absorbed with pelleted Rauscher leukaemia virus, diluted 1:64	—	—
(e) As (b) and absorbed with pelleted Gross leukaemia virus, diluted 1:64	—	—
(f) As (b) and absorbed with pelleted feline leukaemia virus, diluted 1:64	—	—
(g) Controls		
Rat anti-MuLV (gs-3) serum 1:64 followed by treatment with ferritin conjugated normal goat IgG	—	—
Normal rat serum 1:20 followed by treatment with ferritin conjugated goat anti-rat IgG	—	—

NT, not tested.

Virus particles in both cell cultures were labelled by ferritin with the rat anti-MuLV (gs-3) serum (Figs. 2a and b). The labelling was not removed by absorption with Forssman antigens but removed by absorption of the serum with high-speed pellets of either Rauscher leukaemia virus obtained from spleen of infected (CFW-2) mice (obtained from Hazelton Labs), or with gross leukaemia virus obtained from spleen of NIH BALB/c mice (from Germfree Products, Inc.) (Table 1). Absorption with high-speed pellets of feline leukaemia virus (from Electronucleonics, titre 1×10^9 /ml.) also removed the labelling of type C virus particles in both tissue cultures (Table 1). These results indicate that the ESP-1 virus particles share an antigenic determinant similar to the group specific, gs-3 (interspecies antigen) of the mammalian leukaemia viruses^{7,10}.

The presence of the gs-3 antigenic determinant in the ESP-1 virus particles as shown by these tests, compared with the earlier negative results of immunodiffusion tests¹, may be explained by the high sensitivity of the immunoferritin technique. These observations indicate an antigenic relationship between the particles in the ESP-1 human cell culture and those virus particles present in leukaemia and sarcomas of animals.

The presence of a similar group specific antigen (gs-3) in the ESP-1 cell culture is supported by the fixed immunofluorescence test (Prior, unpublished data) using the same rat anti-MuLV (gs-3) serum and rabbit anti-feline leukaemia virus serum (from Dr W. D. Hardy).

We understand that the presence of murine leukaemia virus group specific antigen has been recently observed in the ESP-1

human cell line by immunodiffusion¹¹. Further studies are needed to explain the difference between those results and those of our present findings.

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Antibody and Plant Agglutinins stimulate Phagocytosis of Erythrocytes by *Acanthamoeba*

AXENICALLY grown *Acanthamoeba* phagocytose in simple media a wide variety of particulates while exercising particle discrimination¹, and for studies of particle recognition they provide a useful alternative to vertebrate phagocytes². We have shown that the uptake of sheep erythrocytes (SE) by the amoebae is increased by antibody to the red cells, as with mammalian macrophages. However, the mechanism of opsonization by antibody seems to differ in this case. Furthermore, ingestion of SE by the amoeba was enhanced by plant agglutinins.

Acanthamoeba sp. were supplied by Dr R. J. Neff³, and phagocytosis was assessed microscopically or measured by spectrophotometry of amoeba extracts after osmotic lysis of uningested red cells¹. Rates of uptake⁴ were obtained from absorbances at 30 and 60 min and are expressed in absorbance units/10⁶ amoebae/min. All rates are averages of triplicate determinations. Rabbit antiserum (titre 1:3,200) was obtained after repeated intravenous injections of washed SE.

Whereas control SE were ingested at rates of 0.0001 to 0.0010 in different experiments (0.2 to 2.0 red cells ingested per amoeba in 60 min), addition of antiserum consistently stimulated red cell uptake. In a typical experiment ingestion rate in the controls was below 0.0001; with antiserum added to the amoeba-red cell mixture at dilutions of 1:400, 1:800 or 1:1600, ingestion rates were respectively 0.0174, 0.0113 and 0.0035 units. These results were confirmed by microscopic examination (Fig. 1 A and B). Phagocytosis was increased at serum dilutions that did not result in visible agglutination of red cells. There was also enhancement when the particles were treated with

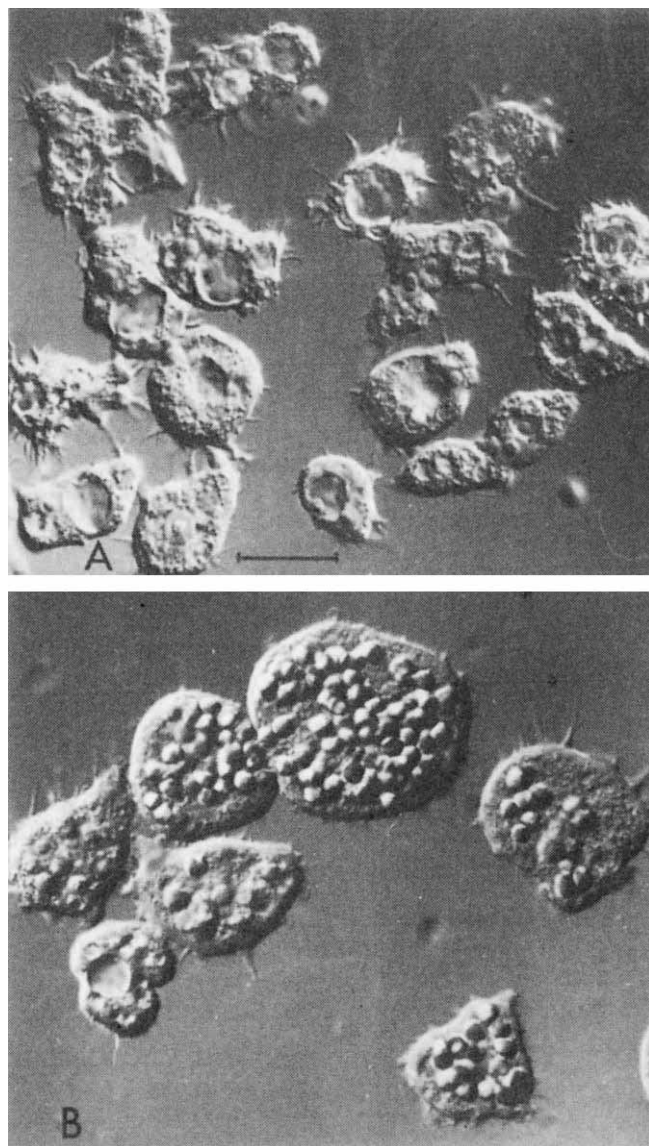


Fig. 1 *Acanthamoeba* incubated with sheep erythrocytes. Zeiss Nomarski optics. Scale line equals 20 nm. A, Control; B, 1:1,000 rabbit antiserum to sheep red cells was added to the amoeba-red cell mixture. Note absence of erythrocytes in A and extensive ingestion in B.

serum and washed before incubation with the phagocytes. The effect of antiserum was ascribed to specific antibody because (a) normal rabbit serum at 1:400 dilution was ineffective; (b) antiserum absorbed with sheep red cells lost its opsonizing activity, and (c) antiserum absorbed with horse red cells was as active as non-absorbed serum. These results are compatible with the report⁵ that the amoeba phase of the slime mould *D. discoideum* grew on certain strains of *Salmonella* only when the bacteria were pretreated with specific antiserum; however, the extent of phagocytosis was not ascertained directly. The results obtained with antiserum could be duplicated with IgG or with IgM-rich fractions prepared on 'Sephadex G-200' by Dr V. Nussenzweig. Binding to macrophages of IgG-coated SE is inhibited by non-immune IgG and is reduced by digestion of IgG with pepsin². Non-immune IgG (0.5 mg/ml.) had no effect on the uptake by amoebae of SE pretreated with antiserum. In addition, Fig. 2 shows that on a protein basis, intact or pepsin-digested IgG (ref. 6) had nearly the same stimulatory activity. Thus, while antibodies stimulated uptake of SE by amoebae, the organism does not seem to possess receptors for IgG comparable to those on macrophages.

Plant agglutinins also increased the uptake of red cells. SE were treated for 60 min at room temperature, washed twice and

incubated with amoeba. With Difco phytohaemagglutinins M (100 µg/ml.) or P (20 µg/ml.) or with concanavalin A (Miles) at 20 µg/ml., ingestion rates were, respectively, 0.0168, 0.0148 and 0.0113, whereas that of control red cells was 0.0001 units. A rate of 0.0030 was obtained when as little as 1.5 µg concanavalin A was added to 7×10^8 SE, or a maximum of about 18,000 molecules of agglutinin per SE (ref. 7). Amoebae pretreated with 10 µg/ml. concanavalin A, washed and incubated with SE, were ingested at rates similar to those of untreated amoebae, indicating that the agglutinin itself was not bound to the phagocytes.

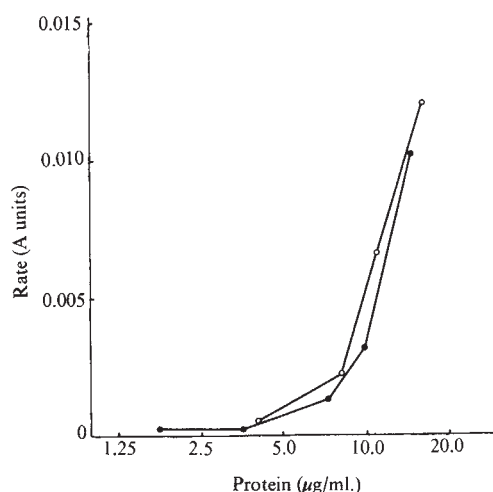


Fig. 2 Effect of control (closed circles) or of pepsin-treated IgG (open circles) on the ingestion of sheep red cells by *Acanthamoeba*. 0.5 ml. of the protein in saline-tricine was incubated with 3×10^8 sheep red cells for 30 min at room temperature; 10^6 amoebae in 0.5 ml. of saline-tricine was added per tube and the mixtures rotated at 22° C for 30 and 60 min. Non-ingested red cells were lysed, the amoeba pellets were washed and extracted with formic acid. Rates are (A 60 min—A 30 min)/30.

Several mechanisms could account for antibody or agglutinin stimulation of SE uptake by *Acanthamoeba*: (1) masking of antiphagocytic substances⁸ that may be present on the SE surface; (2) addition to the SE of materials more likely to interact with the amoebae; (3) modification of the charge or other overall property of the SE in a way that favours particle-phagocyte interaction^{9,10}.

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Inhibition of Attraction and Cross-attraction by Interspecific Sex Pheromone Communication in Lepidoptera

Most studies with lepidopteran sex pheromones have involved the stimulation or attraction of males by known chemicals or extracts of females, but chemicals which are responsible for inhibition of stimulation¹⁻⁴ or attraction⁵⁻⁹ by an active pheromone may be equally useful. These inhibitory chemicals, which are often similar in structure to active pheromones, are effective either simultaneously or before the exposure of the insect to an active pheromone. We now describe a case in which male attraction to females of the same species is inhibited by a pheromone emitted from females of a closely related species.

Our tests were conducted with the Indian meal moth *Plodia interpunctella* (Hübner) and the almond moth *Cadra cautella* (Walker), both phycitid species. Non-mated 2-day-old males were released in closed 43 m³ rooms, under humidity and temperature control, 3 h before live non-mated 2-day-old females were introduced into small cages fitted inside traps constructed from quart-sized cylindrical paper cartons. A slow stream of air was directed through each trap, and 'Stikem' was coated inside the exhaust end of each trap-cylinder. The room was maintained on a 12:12 h light:dark cycle with the scotophase beginning 1 h after introduction of females. In one experiment we tested male attraction to females of each of the two species separately, and in another experiment to females of both species simultaneously. Whether used alone or in combination, fourteen females of each species were used in all tests. When used in combination, females of each species were held in separate traps to test the ability of males to select their own females. Individual tests of the two experiments were conducted alternately.

Our results (Table 1) reveal three distinct occurrences. (1) Indian meal moth males are attracted in equal numbers when only Indian meal moth females are present, only almond moth females are present, or when females of both species are present simultaneously. (2) Almond moth males are attracted to a degree similar to Indian meal moth males when only their own females are present. Almond moth males, however, are only slightly attracted to Indian meal moth females, and when females of both species are present simultaneously in comparison to female almond moths alone, there is a full 70% reduction in the total number of almond moth males attracted. (3) Most attracted males of each species select their own females, when given a choice of the two.

We eliminated visual selection by the males for their own females by installing baffles inside the traps to conceal the females. We also obtained similar selective attraction and inhibition of almond moth males when hexane-ether (1:1) homogenates of the abdominal tips of non-mated 2 day old females on filter paper were substituted for live females inside the traps. These results substantiate that chemical emission from females is the basis for selective attraction by both

Table 1 Effect of Female Moths of Other Species on the Attraction of Male Moths by Females of Their Own Species

Species ♂ tested	Average % ♂ attracted				
	Exposed separately		Exposed simultaneously		Total
	to AM ♀♀	to IMM ♀♀	to AM ♀♀	to IMM ♀♀	
AM	66 ± 6	14 ± 6	17 ± 5	2 ± 2	20 ± 4
IMM	62 ± 3	66 ± 6	7 ± 5	50 ± 5	57 ± 5

Average percentage attraction (± 1 s.d.) of Indian meal moth (IMM) males and almond moth (AM) males after liberation in a 43 m³ closed room, in two types of experiments involving exposure to females of each species separately, and to females of both species simultaneously.

Results of forty-six individual tests. Total of 4,804 male moths tested.

males, and inhibition of almond male attraction by Indian meal moth females.

A component of the sex pheromone from females of both of these species has been isolated and identified as *cis*-9, *trans*-12, tetradecadien-1-yl acetate (I)^{10,11}. This was the only sex stimulatory compound isolated from females of either species. Males of each species, however, are preferentially attracted to females of their own species when females of the other species are present. Further, almond moth male attraction is strongly inhibited in the presence of Indian meal moth females. We feel that these results can best be explained by the release of a multiple component sex pheromone from the Indian meal moth. On the other hand, Indian meal moth females may release relatively large amounts of compound I which is known to inhibit the stimulatory response of almond moth males¹¹. Inhibition of attraction of almond moth males by compound I alone seems unlikely in these tests, however, because of the known small amount of this compound in the above inhibitory extracts of Indian meal moth females. These results along with previous results¹¹ indicate that females of both species emit multiple component pheromones which aid in isolating these species.

Clearly, this demonstration of a naturally occurring inhibition of attraction is significant to use of sex pheromones or pheromone components in the manipulation of insect populations.

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Pseudomonic Acid: an Antibiotic produced by *Pseudomonas fluorescens*

THE antagonistic effects of *Pseudomonas fluorescens* were first recorded by Garre¹ in 1887. Several reports since have dealt with the biological activity of cultures and extracts of *P. fluorescens*². We wish to report the production and purification of these inhibitory substances and the characterization of a metabolite responsible for a significant proportion of the antibacterial activity.

A strain of *P. fluorescens* (a soil isolate, NCIB 10586) was grown in submerged culture at 30° C in a medium containing 1% corn steep liquor and 0.5% glucose in a basic salts solution. The maximum yield of the antibiotic occurred after 24 h and all detectable activity was in the culture fluid. (Activity was measured by the plate assay method using *Staphylococcus aureus* (NCTC 6571) as the test organism.) After the addition of barium chloride (0.5% w/v) the cells and precipitated non-active material were removed by centrifugation. The activity was progressively concentrated by partitioning into isobutylmethyl ketone (IBMK) (0.2 volume) at pH 4.5, water (0.8 volume) at pH 8.5, and then IBMK (0.25 volume) at pH 4.5, followed by evaporation to a small volume under reduced pressure. After a further partition into water at pH 8.5 and adjustment to pH

7–8, the aqueous solution was freeze dried to give a mixture of sodium salts which could be stored at 0° C for several months without loss of activity. Fermentations up to 3,000 l. have been routinely carried out, yielding 1–2 g sodium salts/100 l. culture fluid active at a concentration of approximately 0.1 µg/ml. by the plate assay method.

The antibiotic extract was stable within the range pH 4–9 at 37° C for 24 h. Outside these limits there was a significant loss of activity. The mixture of sodium salts showed a wide antibacterial spectrum against Gram positive and Gram negative bacteria, showed low toxicity and was bacteriostatic against *S. aureus* (NCTC 6571) and *E. coli* (MRE 600). It was haemolytic and inactivated by serum at concentrations >50%.

The crude acid mixture was purified further by chromatography on 'Amberlite XAD-2' polystyrene resin with a linear gradient produced by adding 0.01 N methanolic ammonia to 0.01 N aqueous ammonia. A series of low molecular weight acids was eluted first followed by fractions (30–60% elution) that possessed the major part of the antibacterial (biological) activity. Reaction of these fractions with diazomethane yielded a mixture of methyl esters that could be separated into two fractions by thin-layer chromatography on silica gel (GF₂₅₄) on development with chloroform/isopropanol (9:1). The major fraction (*R_f* 0.4) crystallized from benzene/petroleum ether as colourless needles, melting point 76.5–78° C. Elemental analysis indicated the formula C₂₇H₄₆O₉ (found: C, 62.8; H, 8.9; C₂₇H₄₆O₉ requires C, 63.0; H, 9.0%), and the ester is optically active ($[\alpha]_D^{25} -9^\circ$ (c, 1.5 in chloroform). Analysis of the oily *p*-bromophenacyl ester indicated a formula C₃₄H₄₉BrO₁₀ (found: C, 58.1; H, 6.9; C₃₄H₄₉BrO₁₀ requires C, 58.5; H, 7.0%). Thus the formula of the parent monocarboxylic acid, for which we propose the name pseudomonic acid, is C₂₆H₄₄O₉. Further support for this formula derived from the mass spectrum of the methyl ester which showed the expected molecular ion at *m/e* 514. The infrared spectrum of the methyl ester showed $\nu_{\max}$ (CCl₄) 3,440 (hydroxyl), 1,740 (ester), 1,715 and 1,650 cm⁻¹ (α,β -unsaturated ester). The ultraviolet spectrum, $\lambda_{\max}$ (EtOH) 221.5 nm (ϵ 13,400) confirms the presence of the α,β -unsaturated ester linkage. The nuclear magnetic resonance spectrum showed the presence of two secondary methyl groups (τ 9.09, 8.81), an olefinic methyl group (τ 7.84), a methoxyl group (τ 6.40) and an olefinic proton (τ 4.32).

Acetylation of the methyl ester with pyridine/acetic anhydride affords a triacetate C₃₃H₅₂O₁₂, which absorbs 1 mol of hydrogen giving a dihydro derivative C₃₃H₅₄O₁₂, on catalytic hydrogenation, showing only end absorption in the ultraviolet. Reduction of the methyl ester with LiAlH₄ in tetrahydrofuran afforded 1,9-dihydroxynonane, melting point 46°, *bis*-phenylcarbamate, melting point 168–9° (melting point³ 42.5–44.5°; *bis*-phenylcarbamate, melting point³ 171.5–172.5°). Treatment of the *p*-bromophenacyl ester with KMnO₄/NaIO₄ gave *p*-bromophenacyl-9-hydroxynonanoate, C₁₇H₂₃BrO₄, m.p. 77.5–78° (found: C, 55.1; H, 6.4; C₁₇H₂₃BrO₄ requires C, 55.0; H, 6.2%). Mild base hydrolysis of the methyl ester yielded methyl 9-hydroxynonanoate (oil) C₁₀H₂₀O₃. Further confirmation of the presence of the 9-hydroxynonanoate unit in pseudomonic acid is provided by the mass spectrum of the methyl ester. Mass measurement of the fragment at *m/e* 327 gave 327.18059 (C₁₇H₂₇O₆ requires 327.18075) corresponding to the loss of $-\text{O}(\text{CH}_2)_8\text{CO}_2\text{CH}_3$ from the molecular ion.

Thus pseudomonic acid contains the biogenetically unique 9-hydroxynonanoic acid, the hydroxyl group of which is joined to the rest of the molecule through an α,β -unsaturated ester linkage. The structure of pseudomonic acid and other biologically active metabolites of *P. fluorescens* is under investigation.

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Infectious Pancreatic Necrosis in Rainbow Trout in Scotland

INFECTIOUS pancreatic necrosis (IPN), a highly contagious viral disease of young trout, endemic in wild salmonids and some trout farms in the United States, and first recorded in Europe in 1965¹, has now been positively identified as causing an epizootic of rainbow trout fry (*Salmo gairdneri*) in a Scottish trout farm during February and March this year.

The signs seen in this outbreak were typical², general dorsal darkening, swollen abdomen and the white mucous filling the stomach and intestine. Stained sections (haematoxylin and eosin) of the pyloric caecal area showed severe necrosis of the pancreatic tissue, which was well infiltrated with macrophages and in some cases almost completely degenerated. For electron microscopy, pancreatic tissue from diseased rainbow trout was fixed in osmium tetroxide in veronal buffer³, dehydrated through an ethyl alcohol gradient and embedded in 'Araldite'. Ultrathin sections were cut on an LKB Ultratome III using glass knives and mounted on uncoated grids. They were stained by the alkaline lead oxide method⁴ and examined in a Siemens Elmiskop I using the double condenser system and an accelerating voltage of 60 kV. IPN virus particles were found, both distributed randomly in the cell cytoplasm and in cells with areas of necrosis, in membrane-bound aggregates 1–3 µm in diameter (Fig. 1). The virus particles were hexagonal in profile, averaging 55 nm in diameter and, in some membrane-bound aggregates, arranged in crystalline arrays^{5,6} (Fig. 2).

The virus was isolated in 1–3 day-old RTG2 (rainbow trout gonad) and FHM (fat head minnow) cell lines kept at 20° C and infected with filtered (0.22 µm 'Millipore') complete fish homogenates of distressed fish (diluted to about 1:50 in Hanks BSS). The isolate has been passaged several times.

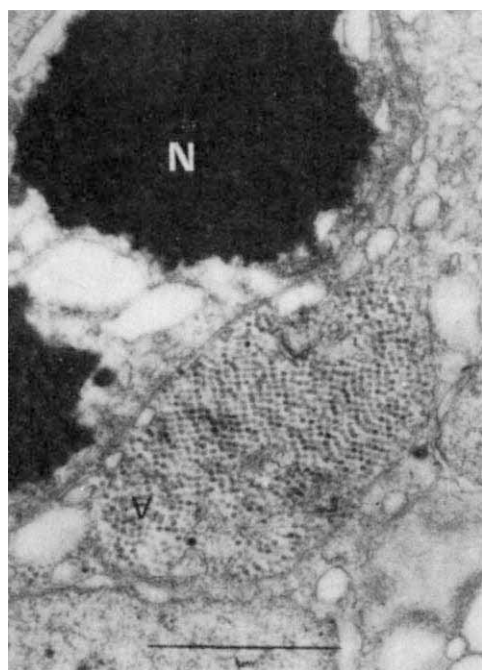


Fig. 1 Electron micrograph of ultrathin section of rainbow trout pancreatic tissue. Part of a cell showing necrotic area (N) and viral inclusion (V). Marker, 1 µm.

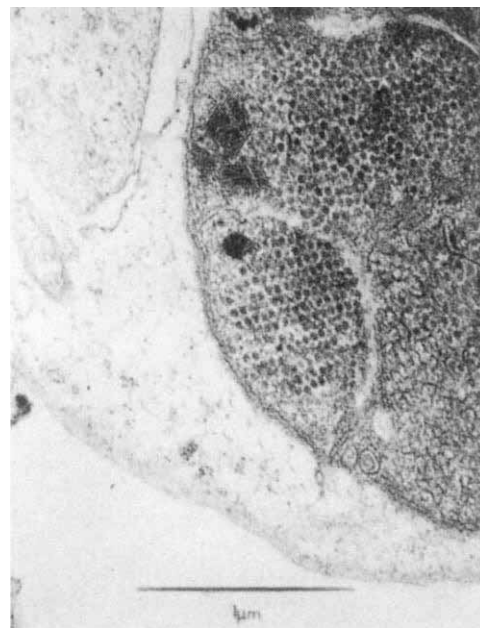


Fig. 2 Electron micrograph of an ultrathin section of rainbow trout pancreas. IPN virus particles showing early stages of crystal lattice formation. Marker, 1 µm.

Supernatant cell culture fluid from the fifth passage was added to water containing sea trout fry (*Salmo trutta*) which had just commenced feeding. Fry mortality with most of the gross pathological signs were noted from the sixth day, pancreatic necrosis was confirmed in sections and the virus was isolated in RTG2 cells from moribund whole fish.

Characterization of the virus as IPN included a serum neutralization test using goat anti-IPN serum (Microbiological Associates, Inc.). This serum is specific for strain VR299 (American Type Culture Collection) of IPN virus; it delayed the occurrence of a cytopathic effect in RTG2 cells but did not prevent it. Survival in 10% ether and 50% glycerol (the latter for 1 month) was demonstrated⁷.

The farm where this outbreak occurred is comparatively new and has received only four shipments of eggs, all from one supplier in Denmark. The disease occurred in fry hatched from the second shipment which arrived in late September 1970 and which started to feed in late January. Mortalities were noted in increasing numbers from mid-February onwards. These events implicate the eggs as the means of transmission of the virus as has been suggested by others⁸. It is interesting to note that this early winter spawning strain, which was introduced from France and America, is thought to be the origin of IPN in Denmark⁹.

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Syntactic Class as a Determinant of Word-retrieval in Normal and Dyslexic Subjects

SUBJECTS with dyslexia following brain lesions may read concrete nouns significantly better than other parts of speech¹. There may be a normal analogue in tachistoscopic recognition thresholds for different parts of speech. The only study in which this has been investigated², however, was conducted with German adolescents, and the results may have been biased by a difference in the relative usage of concrete nouns by adolescents and adults.

We have conducted similar experiments on syntactic class effects in English, and have investigated the reading performance, on the same material, of a small group of subjects with residual acquired dyslexia. A list of sixty words, consisting of twenty concrete nouns, twenty adjectives and twenty verbs, was used. The words vary in length between four and seven letters, and are divided into five frequency ranges (Thorndike and Lorge³). All words are matched for length and frequency across the three syntactic classes; there are equal numbers of words in all frequency ranges and at all lengths.

In the first experiment, these stimuli, typed in lower case (Delegate typeface) letters, were presented individually in a three-channel tachistoscope (Scientific Prototype, MFG Corp, model GB). The subject fixated a central cross in the pre-exposure field, and, after a "ready" signal, the stimulus was presented centrally, followed by a blank post-exposure field. An ascending method of limits was used; the first exposure was 10 ms and on each successive exposure the duration was increased by 5 ms until the subject correctly reported the stimulus on two consecutive trials. Order of presentation of the sixty stimuli was randomized anew for each subject. Practice trials were given to familiarize the subject with his task. The subjects were twenty students, technical and academic staff of the University of Edinburgh (mean age 24 yr). The results are shown in Table 1. Friedman two-way analysis of variance shows that the effects of syntactic class, length and frequency are significant at beyond the 0.001 level. The difference between nouns and verbs is significant (Wilcoxon matched-pairs signed-ranks test, $T=2$; $P<0.001$, two-tailed), as is the difference between nouns and adjectives ($T=40.5$; $P<0.02$, two-tailed) and adjectives and verbs ($T=27$; $P<0.01$, two-tailed).

To check that these results are not due to uncontrolled (and at present uncontrollable) variation in the purely visual properties of the stimuli, a second experiment was conducted using the same words in upper case (Delegate) letters. Seven subjects from the same population as before (mean age 20 yr) were tested. The initial exposure was 10 ms, increasing by 10 ms on each trial. In all other respects, the experimental method was the same as in experiment 1. The mean recognition thresholds for the syntactic classes were: nouns, 37.0 ms; adjectives,

41.4 ms; verbs, 45.2 ms. Friedman two-way analysis of variance shows that these values are not drawn from the same population ($Xr^2=7.36$; $P<0.05$). The difference between nouns and verbs is significant at the 0.05 level ($T=0$). With such a small number of subjects, the noun/adjective and the adjective/verb differences fail to reach significance. The upper case means are higher than lower case, as is customarily found, but the effect of syntactic class is still demonstrable.

The same words, in lower case, were presented for reading aloud, to five dyslexic subjects, mean age 48 yr. All five men received penetrating missile injuries to the left hemisphere during the Second World War. All have residual language impairment with a disorder of reading being one of the predominant features (for further details of these cases, see Marshall and Newcombe⁴). The words were presented, individually typed, on plain white cards. No time pressure was imposed. The subjects read correctly eighty-one nouns (out of 100; twenty nouns, five subjects), fifty-five adjectives and fifty-four verbs ($Xr^2=6.3$; $P<0.05$). The effects of length and frequency are significant at beyond the 0.01 level. Thus a number of stimulus variables which affect tachistoscopic recognition thresholds are also correlated with dyslexic performance.

The order of difficulty in syntactic class (verb > noun) and over the frequency ranges (infrequent > frequent) is the same in both the dyslexic and the normal subjects; but increasing length (between four and seven letters), which is correlated with a lowering of threshold in the normal subjects, resulted in increased difficulty for the dyslexic subjects. A further difference is that thresholds for adjectives for the normal subjects are intermediate between nouns and verbs, while for the dyslexic subjects reading-performance on adjectives is indistinguishable from that on verbs. (Halpern¹ has also reported this latter result.)

The next task is to discover how and why the observed facilitation of nouns takes place.

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Lateral Thinking about Lateral Inhibition

It has recently been asserted¹ that the well known apparent expansion of acute angles is due not to the lateral inhibition proposed by Blakemore *et al.*², but to an adaptation effect similar to the Gibson tilt after-effect^{3,4}. The arguments by which Coltheart arrives at this conclusion, however, seem to us to be based on a complete misreading, and hence misrepresentation, of our article, which we should like to correct.

The strongest reason for rejecting adaptation as an explanation for angle expansion is, as Coltheart correctly adduces, the fact that disinhibition (that is, partial cancellation of angle expansion) may be produced by introducing a third line into the figure. Coltheart proceeds to discuss the special case in which the disinhibiting line lies outside the angle in question,

Table 1 Mean Recognition Thresholds in Milliseconds

Syntactic class	Nouns 30.3		Adjectives 33.3		Verbs 35.8	Xr^2 21.63 *
Length (in letters)	Four 39.5		Five 31.7	Six 32.1	Seven 29.9	57.8 *
Frequency	AA 27.5	A 27.1	37-17 30.0	18-8 39.4	8-1 41.6	40.9 *

* $P<0.001$.

and states, again correctly, that both adaptation and inhibition would reduce the degree of apparent expansion. He does not consider the more informative and critical case where the disturbing line lies inside the angle. Here, adaptation and disinhibition predict exactly opposite effects. Our own experiments show that disinhibition occurs equally strongly whether the third line is inside or outside the angle; it is for this reason, primarily, that we reject the adaptational explanation.

In any case, Coltheart's argument assumes that it was the apparent size of the angle as a whole that was measured. Our paper makes it perfectly clear that our observations were on the apparent orientation of the arm of the angle further from the third line, and not on either the nearer arm or the angle as a whole. His argument is therefore fallacious as well as incomplete.

Coltheart comments unfavourably on the difference between the usual angular distributions of inhibition commonly obtained in orientation-masking studies, and our Fig. 1 (ref. 2), but this figure does not, as he seems to suppose, represent the spread of inhibition from a single line, but rather the total pattern of activity, combining both excitation and inhibition, which both fall off monotonically from the optimal orientation, as is stated explicitly in our paper: the trough at 6° occurs because the excitation falls off more rapidly than the inhibition, and has nothing to do with maximal inhibition or maximal masking. There is therefore no discrepancy to explain.

Finally, we are at least grateful to Coltheart for pointing out the remarkable similarities between the simultaneous angle expansion and the successive tilt after-effect. Their magnitudes, directions, and even their time-courses are similar. This leads us now to propose that far from the simultaneous effect being due to some ill-defined "adaptation" or "satiation" of orientation detectors, the Gibson after-effect itself may be due to the long-lasting consequences of prolonged inhibition. Adaptation may be due to lateral inhibition, but certainly not the reverse.

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Paradox with After Images

A FEW years ago, experimenting with the crisp after images that are left by an electronic flash, I noticed something which surprised me since it seemed to contradict views about after images in relation to dark adaptation.

Only recently have I seen that some very obvious considerations resolve the paradox, and the "surprising feature" is just what common sense should have led one to expect. Though I confess it has taken me a long time to see the obvious, I have little doubt that many readers will see it as soon as they try. Therefore this week I present the paradoxical observations; the week after next I shall give experiments to support the rather obvious resolution.

To make the paradoxical observation the eye is bleached by an electronic flash presented in Maxwellian view (Fig. 1a). The flash tube is at the focus of lens L_2 and the subject's pupil at the focus of lens L_1 . In the collimated region between L_1 and L_2 is a circular aperture (Fig. 1b) divided into three regions by the interposition of neutral densities meeting at lines set at

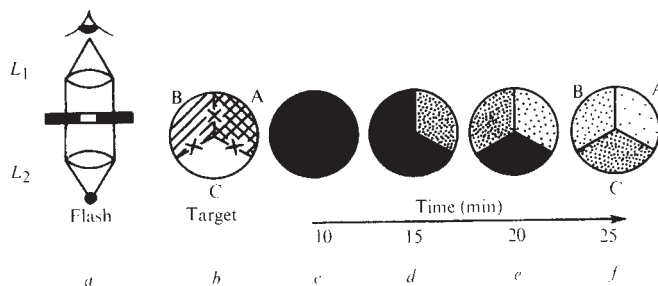


Fig. 1 a, Electronic flash collimated by lens L_2 and presented to eye in Maxwellian view by L_1 . Interposed mid-way is the tripartite filter shown in b. Sectors A, B, C are neutral densities 0.5, 0.2, 0.0 respectively. The centre is fixated and areas A, B, C of retinal image differently bleached. c-f represent the appearance of the negative after image seen by momentarily opening the bleached eye and viewing a faintly illuminated white wall. At 10 min (c) the image is uniformly black; at the subsequent times shown, it breaks up into sectors and gradually fades in blackness.

120 with each other, the densities being 0.0, 0.2 and 0.5. The demarcation lines are seen sharply, and after discharging the flash they are at once conspicuous in the cone after image which follows. Ten minutes later the cone image has faded beyond recall, but the grey rod after image may be recalled for a further 15 min.

A good way to recall after images is to blink in a room dimly lit. When the eyes are shut we see a positive after image, which is a faint replica of what was seen during the flash. When the eyes are opened we see against the white wall a negative after image, the same picture as the positive but with contrast reversed like a photographic negative. In my experiment the eyes were kept shut and opened for a second or so from time to time, and the negative after image was thus seen against the white wall.

The surprise is that the proper negative of Fig. 1b is not seen until Fig. 1e, 18 min after the flash. At 10 min all we see is a black uniform circular patch without subdivision. At 15 min suddenly a lighter portion separates out (Fig. 1d) corresponding to the retinal region bleached through 0.5 filter, and this portion continues to get lighter and lighter, the black part remaining unchanged. At about 18 min suddenly the black part shows a demarcation line (Fig. 1e) and the region bleached through the 0.2 filter starts to get lighter. Finally the most strongly bleached retina slowly pales and the rod after image finally fades away.

If we consider these changes in reversed time, going from (f) to (e) of Fig. 1, all three sectors get darker as pigment regeneration is less advanced. But evidently the intensity of after image does not increase indefinitely. In each sector there is a fixed ceiling of intensity above which the image cannot go. The lowest sector (C) is most bleached, and hence is first to reach the ceiling (going backwards in time). By Fig. 1d sector B has also reached the ceiling, and at 10 s (Fig. 1c) the whole area is at the same ceiling level.

Now Barlow and Sparrock¹ showed that at every stage in dark adaptation, the log threshold for test flash detection (the ordinary dark adaptation curve) is raised in proportion to the log brightness of the after image, which they claim is the immediate cause of the familiar desensitization by bleaching. If there is a ceiling to the intensity of the negative after image, either there must be a corresponding plateau in the rod dark adaptation curve, or else this image intensity cannot be the cause of the threshold rise. Fig. 2 shows dark adaptation curves in the experiment which gave the images of Fig. 1. There were three small red fixation points set in an equilateral triangle and the small test flash fell at its centre. When immediately after the bleaching flash I went into the dark adaptometer and fixated on the centre, I saw the positive (cone) after image and the three fixation points at the places marked by crosses on the radii, Fig. 1b. Thus fixating in turn on each red light permits the test flash to fall in the middle of the three bleached regions. Fig. 2 shows the three rod dark adaptation curves each preceded

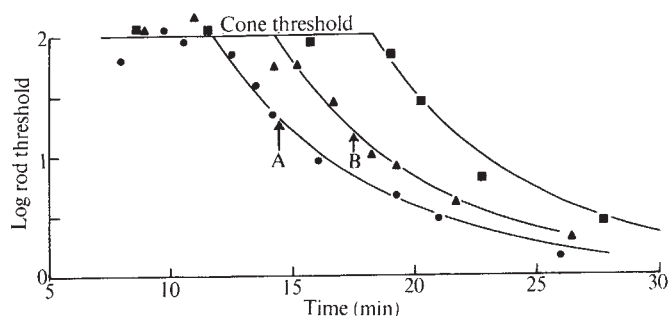


Fig. 2 Dark adaptation curves, that is, log threshold for test flashes plotted against time after the bleaching flash. Curves A, B, C plot measurements when the test fell near the middle of bleached areas A, B, C respectively of Fig. 1b. Curves drawn through rod branches are the exponential with half decay time of 4.5 min. Arrows A, B mark the moment when the appearance of the after image changed from Fig. 1c-d and d-e, respectively.

by a cone branch. They are normal rod curves, each being an exponential that falls to half in 4.5 min. The vertical arrows A, B indicate the moments when sector A separated itself (Fig. 1d) and segment B separated (Fig. 1e).

It is plain from Fig. 2 that the arrows, which mark the ceiling of after image intensity, correspond to a fixed ordinate in the dark adaptation curve, a fixed threshold rise above the full dark value. But it does not correspond to any flattening or ceiling of threshold rise. If Barlow and Sparrock¹ were correct in saying that the intensity of our after image was the immediate cause of the threshold rise, how could thresholds continue to rise to the left of the arrow in Fig. 2 though the after image remains unchanged in intensity?

I think many readers will be able to answer this. The week after next I shall give experimental confirmation of what they probably expect.

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Conservation of Water-damaged Written Documents by Freeze-drying

ECONOMIC considerations generally eliminate freeze-drying as a practical method for the drying of paper materials. Although we are aware of accounts in the literature about the freeze-drying of paper materials (generally filter paper) we have not seen any references to work on the freeze-drying of written documents for conservation purposes.

While a fire was being extinguished at the Greenland Regional Library in Godthåb during the winter of 1968, many valuable items (hand-written manuscripts, books, letters and so on) became wet and subsequently froze. The damaged items were transported in their frozen state to Copenhagen and held there for 2 yr while a decision was made about the drying method to be adopted. Most of the printed books were air-dried in the conventional manner, with good results considering the circumstances.

The more valuable items were hand-written letters, manuscripts and maps belonging to a mid-nineteenth century missionary to Greenland, Samuel Kleinschmidt. It was felt that the ink used in these documents would run during the melting associated with an air-drying process, thus ruining them. Our laboratory was therefore asked to undertake the freeze-dehydration of the frozen written materials.

Some preliminary experiments with modern papers and writing materials were conducted to gain some experience in handling frozen hand-written materials. These experiments

showed that temperatures up to at least 110° C can be tolerated for several hours without discoloration of the paper. The advantage of freeze-drying was made clear by a comparison experiment in which paper marked with various modern writing materials (ink, ballpoint pen, felt-tip marking pen) was immersed in water, frozen and then dried. The freeze-dried sample was perfect, whereas the writing on the air-dried sample had run.

The twenty-seven storage packets in the Kleinschmidt collection and a photograph album were transported from the Copenhagen branch of the Greenland Regional Library to the Food Technology Laboratory in insulated containers cooled with dry ice. The papers were held at -30° C until prepared for freeze-drying. The storage packets were tight fitting paper and cardboard holders of the standard type used in libraries for filing loose papers. A preliminary trial showed that, by careful manipulation of the frozen packets, these holders could easily be removed thus eliminating a large resistance to mass transfer in the packet. Both to facilitate the rate of drying and to ensure sufficient clearance between the heater shelves, some packets had to be prised apart while frozen. This was made easier by the fact that the packets consisted of groups of paper folders. Stacks of the prepared frozen papers 2 to 3 cm thick, were placed on pre-cooled, porous sample trays and conservative freeze-drying conditions were chosen so that no melting or colour change could occur. Radiant heating at a plate temperature of 45° C and a chamber pressure of 200 mtorr was used. The sample weight was monitored using the balance built into the freeze-dryer (Atlas Ray 1) and drying was continued to constant weight. The average drying time in these conditions was about 1.5 to 2 days and when the drying was complete, the chamber vacuum was slowly released.

The drying process gave perfect results for all the written paper documents. Each page separated easily and in no case did the ink run. A few of the envelopes were stuck together as some of the old wax seals had softened (probably due to the use of the elevated heating temperature). They separated on cooling though some transfer of the wax colour had occurred. It was observed that packets (usually the thicker notebooks) which had been compressed into certain shapes before freezing retained the principal features of that shape after drying; and because of the pressures which developed there was a tendency for the packets to expand like an accordion as they dried. These misshapen samples were later treated in the usual manner of pressing and rebinding.

The photograph album presented more problems, the most serious of which was the tendency of those prints which were frozen emulsion to emulsion, to stick together after drying. Whenever possible, the groups of dried prints that were stuck together were removed from the album, soaked in water and then carefully pulled apart under water. This was usually successful, although in a few cases small portions of the pictures were destroyed. An ordinary darkroom photoprint dryer was used for drying of the separated prints.

The thickness of the photoalbum (10 cm) demanded freeze-drying for 4.5 days. This time was, however, found to be slightly too short, for a group of six pictures located on the centre page was still frozen together at that time. They unfortunately melted before they could be reinserted into the freeze-dryer, ruining the ink hand-written captions. This showed that freeze-drying had indeed been necessary to successfully conserve the written documents.

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BOOK REVIEWS

Cells and Cancer

The Cell Cycle and Cancer. Edited by Renato Baserga. Pp. xii+481. (Marcel Dekker: New York, June 1971.) \$29.50.

I DO not recollect having previously reviewed a scientific book on a topical subject which carried on its jacket a reproduction of a Renaissance painting. The departure in this instance may reflect the tastes of Dr Baserga, whose own contributions to the volume are liberally sprinkled with classical allusions. The editor's imprint on this volume is unusual in another respect in that, instead of writing a formal introductory chapter, he has interspersed the twelve chapters with explanatory and introductory sections. This practice, which Dr Baserga attributes to one of his teachers, might well be copied by editors of other symposium volumes. The reason for these connecting sections, of course, is to try to link together the chapters written in different styles by different authors. In fact, this particular book concentrates on one relatively small topic and, therefore, is quite coherent. Indeed its principal shortcoming is that there is a fair amount of overlap in it; for example, the labelled mitosis method for studying the cell cycle is described many times. This repetitiveness, which may be unavoidable in a volume of this kind, is the chief criticism one can make of it.

The book contains twelve excellent essays on different aspects of the cell cycle, which among them provide an almost complete review of the subject. The first three chapters, by Lipkin, Blackett and Mendelson and Takahashi, are concerned with mathematical aspects of cell cycle kinetics. The next three chapters are concerned with the cell cycle in different normal and diseased states. The cell cycle in cancer cells is discussed by Gavosto and Pileri, in differentiation by Malamud and in response to hormones in different organs by Epifanova. The next four chapters are concerned chiefly with biochemical aspects of the cell cycle. Cooper discusses biochemical alterations accompanying the initiation of growth; Vendrely, cytophotometry and histochemistry in the cell cycle; Mueller, biochemical aspects of the G1 and S intervals; and Tobey, Petersen and Anderson, the biochemistry of G2 and mitosis. Most of the first ten chapters

are devoted to reviewing material, much of which has previously appeared in other books. The eleventh chapter, by Skipper, on the cell cycle and chemotherapy of cancer, is refreshing in that it not only analyses this topic, but also introduces some new ideas about it. The final chapter, on radiobiology and the cell cycle, by Frindel and Tubiana is an excellent, comprehensive review of this large and complex subject.

This is a first rate source book for people working on aspects of the cell cycle. Most of the discussion is at a fairly advanced level and the views expressed seem generally sound. I would take issue with only one or two points (both of those mentioned voiced by the editor). Is it really true that the theory of contact inhibition has been demolished and, by implication, has nothing to contribute to the understanding of cancer (page 55)? Is there justification for suggesting that the differential effects of hydroxyurea on cells in S phase and in G0 may indicate both a metabolic diversity between G0 and G1 cells and that the S phase may be different in different cells (page 191)?

What general impression does one gain about the field by reading this book? My impression is that, although an enormous amount of work of very high quality has been done, we are only a little further forward in the understanding of the mechanism of the cell cycle than we were in 1963 when Howard and Pelc described it. What we have perhaps come to appreciate is the great complexity of the problems. The reproduction on the front cover is of Raphael's St George and the Dragon. St George's allegorical identity is obscure but I imagine the dragon represents the cancer problem. Is the maiden praying for divine intervention in the background possibly intended to represent scientists engaged in studies of the cell cycle?

JOHN PAUL

Receptor Physiology

Principles of Receptor Physiology. Edited by W. R. Lowenstein. Pp. xii+600. (Springer-Verlag: Berlin and New York, 1971.) 134.40 DM; \$37.

The Handbook of Receptor Physiology, to be compiled in eight sections, of which this volume is the first, will repre-

sent a major achievement in the literature of physiology.

The ability of the cell or organism to perceive, analyse and react to external stimuli is clearly one of the most important functions of living systems: in particular, the property of chemosensitivity must have been of early evolutionary significance. The wide variety of incoming stimuli has necessitated the development of a large number of sensory receptors, all of which serve directly or indirectly to transduce the incoming stimuli into trains of sensory impulses, a common output, a fact recognized by Adrian almost fifty years ago and expressed in the frequency code hypothesis. The various transducing mechanisms pose a well recognized and inspiring challenge to which workers in many disciplines are responding with vigour. Unquestionably, more remains to be learnt than has been learnt hitherto and as Ottoson and Shepherd (chapter 15) note for the well investigated muscle spindle, "the basic questions underlying the transducer process are still kept by the spindle as a well guarded secret of its own". The exquisite sensitivity of many transducer mechanisms (insect sex pheromones, reptilian heat receptors) poses the additional question of what molecular gyrations can be responsible for detecting and responding to such low level stimuli? The wide range of input stimuli to which the sensory systems react poses another severe challenge to the understanding of these input-output systems.

This volume is designed to serve as an introduction to receptor physiology by introducing a selection of topics, some of which will be covered in greater detail in subsequent volumes, and which are intended to introduce and survey the field of receptor physiology. This volume includes seventeen chapters dealing with general characteristics of excitable cells, mechanochemical transducers, light perception mechanisms, the analysis of stimulus intensity and peripheral receptor organization. Nachmanson's chapter deals with the roles of the proteins of the acetylcholine receptor in transducing bioelectric events: it contains much useful information on the fruitful applications by Changeux and others of the allosterism concept to chemically sensitive membranes. Yet much of the chapter is

devoted to a further restatement of Nachmansson's views on the general role of acetylcholine in nerve impulse propagation. This particular controversy is too well known to require additional comment here. The immediately subsequent chapters (Tauc and Grundfest) deal with chemical transmitter action in a number of excitable systems and, in typically clear fashion by Grundfest, with the general electrophysiology of the specialized input membrane in excitable cells.

The general relationships between sensory intensity and stimulus analysis are well dealt with by Lipetz and Stevens; the latter presents a stimulating discussion of the Weber-Fechner hypothesis and more recent power function analyses to correlate sensory intensity analyses. Two chapters deal with visual perception: that by Cone and Pak deals very adequately with the origin of and basis of the early receptor potential and Feinleib and Curry discuss phototaxis in plants. As these authors note, the phototactic system may represent a very simple receptor-effector relationship which is, despite past failures, well suited for a complete input and output analysis. The recent discovery of retinal bound to an opsin-like protein in *Halobacterium holobium* (D. Oesterhelt and W. Stoekenius, *Nature New Biology*, **233**, 149; 1971) and its similar orientation in the membrane (A. E. Blaurock and W. Stoekenius, *Nature New Biology*, **233**, 152; 1971) to that in vertebrate retinas suggests the validity of examining simpler biological systems.

I have one major criticism of this book: in a series of topics all of which relate to the cell membrane in some respect it seems an oversight not to have included a specific chapter on the structure and function of cell membranes. There are a number of minor misprints but these do not detract from the high quality of the book. Its price is unfortunately too high to place it in the hands of many individuals. This is a pity, for the book deserves wide circulation. It is an excellent introduction to the proposed series and editors and authors alike are to be congratulated. Subsequent volumes will be eagerly anticipated.

D. J. TRIGGLE

Biochemical Evolution

Biochemical Evolution and the Origin of Life. Edited by E. Schoffeniels. (Proceedings of the International Conference on Biochemical Evolution.) (Molecular Evolution II.) Pp. xiv + 398. (North-Holland: Amsterdam and London, 1971.) £8.40.

THIS volume contains papers on a variety of topics in speculative and comparative biochemistry. They range

from careful statistical studies of the rate of evolution of protein sequences to highly speculative histories, for example of the evolution of metabolic pathways. Some of the papers are excellent, but others are of doubtful value; they provide a good sampling of the field, both with respect to subject matter and quality.

It is clear that the students of protein sequences have many more data on which to base their theories than those who work on other branches of biochemical evolution. The paper by Margoliash, Fitch and Dickerson provides a definitive summary of the conclusions that can be drawn from the extensive series of cytochrome c sequences that have been determined so far. Other interesting papers deal with fibrinogen and immunoglobulin sequences.

The evolutionary biochemistry of small molecules is a much more difficult subject. However, it is at least as interesting, since it provides the only hope of understanding evolution in the period before the major outlines of biochemistry became fixed. Unfortunately, the law of pure cussedness applies in this area: the more primitive the process, the more difficult it is to say anything definite about its evolution. The phosphagens and phosphagen kinases must be comparative newcomers to the biological scene; Watt's discussion of the subject is fairly convincing. Energy production, on the other hand, must be a very primitive process; Broda's interesting treatment of bioenergetic evolution raises as many questions as it answers.

The expert will encounter some new material in this book and much that he has seen before. The general reader should find it a useful introduction to the subject.

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Biochemical Text

Cellular Biochemistry and Physiology. By N. A. Edwards and K. A. Hassall. Pp. xiv + 442. McGraw-Hill: Berkshire, September 1971.) £3.95.

I REMEMBER a friend who was a physicist telling me that his initial test of the value of a dictionary was to look up the entry for "entropy". As might be expected, I tend to look first at the preface of a textbook of biochemistry and then at the chapter on the biosynthesis of proteins.

In the case of the present book I followed this scheme with rather disastrous results. I was with the authors so far as their aim was concerned, for I am sure that many students like their biochemistry to be based on cell physiology and ultrastructure. The chapter entitled "Polynucleotides and Protein Synthesis" is, however, an awful

mess and makes one wonder whether the authors really understand their subject. A typical statement is (page 346): "Under normal conditions, ribosomes not aggregated in this way make little or no protein although, in the presence of an excess of messenger RNA, single ribosomes synthesize protein quite adequately". Their explanations of the structure of DNA and RNA, the way in which Kornberg polymerase effects the synthesis of DNA, and the steps in the attachment of amino-acid to tRNA, to mention just a few points, are very confusing. It really hurts to see such a beautiful story spoilt in this way.

The first chapter on the cellular basis of life would hardly encourage a student to read on, but if he did he would get to proteins, peptides and amino-acids. There is an amazing diagram showing amino-acids hanging from a thread followed by Table 2-1 giving tests for amino-acids (Sakaguchi, Millon and so on). The latter is just the kind of material the authors promised to exclude. The major considerations that led to the concept of the α -helix are not mentioned and Fig. 2-8 is original but not helpful. Do we really have to speculate that the tertiary structure of a protein is the inevitable consequence of the primary structure?

In the chapter on mitochondrial electron transport and oxidative phosphorylation, instead of explaining the objective of the whole business, followed by redox potentials, these matters are left to be described relatively late in the chapter. What happened to "fumarate" in Fig. 6-1? The book ends with a "systematic classification of enzymes" and a very poor list of references.

The authors had a worthwhile objective but in my view they have failed. The book is not to be recommended to students, but we need not be too unduly worried, for it seems very unlikely that a student wanting an elementary text would pay £3.95.

P. N. CAMPBELL

Estuarine Ecology

Ecology of Estuaries. By Donald S. McLusky. Pp. viii + 144 + 8 plates. (Heinemann: London, October 1971.) £1.60.

ESTUARIES are complex and variable environments. A recent symposium on estuaries held in America resulted in a volume containing more than 700 pages, with little overlap in the subject material of the various authors. In a book aimed at sixth formers and first year university students, Dr McLusky has made a brave attempt to provide a concise account of the ecology of estuaries in less than 150 pages. I think

he has succeeded. The style is clear, and the general principles of estuarine ecology are well explained, but condensation has meant oversimplification to the point of error in some places. Estuarine plants are dealt with in four pages, and it is implied that there is a simple gradient of water logging in salt marshes. In fact one frequently finds that the *Juncus* zone at the top of the marsh is more water logged than the middle zones, so that algae present on the lowest part of the marsh reappear on the upper marsh, although absent from the middle.

In general the information in the book is accurate, but there are a few errors. The diagram of the burrow of *Arenicola* shows a simple U-tube open at both ends, and on page 40 it is stated that *Nereis diversicolor* appears to avoid low salinity regions.

References in the text are always a problem in a book of this type, and their use in the present volume is erratic. No references are given in the text of the chapter on plants, but a considerable number are given in the chapter on animals. A point which I found disturbing was the attribution of some figures to secondary sources rather than to the primary ones. For example, Fig. 14 is attributed to Kinne, but Kinne correctly attributes it to Pantin; Fig. 16 is attributed to Lockwood, but Lockwood himself correctly attributes it to Ellis. Even in the text at one point the well known work of Wells, on the oesophageal pacemaker of *Arenicola* is attributed to a secondary source. These points are probably more important to the advanced reader who likes to know who actually did the work.

In spite of these criticisms of details the book will be most useful as a first introduction to the ecology of estuaries.

J. GREEN

Hydrides

Hydrides of the Elements of Main Groups I-IV. By E. Wiberg and E. Amberger. Pp. xv+785. (Elsevier: Amsterdam, New York and London, September 1971.) Dfl. 290.00; £33.85; \$80.75.

THIS is a scholarly and comprehensive monograph which provides a detailed and reliable source of information on all aspects of the chemistry of the hydrides of the elements in main groups I-IV. The authors are internationally respected authorities in this field and their coverage of over 3,500 original references extends to 1970.

The book is extremely well organized and the skilful use of diagrams and tables enables a tremendous amount of factual information to be recorded while leaving the cursive text free to develop the significance of the data. Only in the

introductory chapter (twelve pages) does this approach fail—the compression here is so great that the general review of hydride chemistry, the presentation of theoretical models of hydrides and the general summary of preparative procedures are less informative than many accounts in undergraduate textbooks.

The unique feature of the book is the extensive and perceptive discussion of the chemistry of the hydrides; there is a depth of understanding and insight here which is a welcome change from the approach in many recent books. Too often these days there is an apparent belief that inorganic chemistry begins and ends with a description of the spectroscopic and structural properties of complexes, and little regard is paid to the synthesis, reactions and reactivity of the compounds being discussed. It is refreshing to see some chemical chemistry again.

Two chapters deal successively with the hydrides of the alkali metals (30 pages) and the alkaline earth metals (38 pages). Each starts with a brief historical introduction and general review of the group, followed by a detailed discussion of the preparation, physical properties and chemical reactions of the hydrides of the individual elements.

The most extensive chapter (274 pages) concerns the boron hydrides. These compounds and their derivatives have been much reviewed in recent years but this new approach to their chemistry adds a new dimension to the literature on the subject which undoubtedly enhances our understanding of their subtle and intricate chemistry. Some 170 pages are devoted to synthesis, conversions, reactions and mechanistic schemes and this is followed by extensive tabulation of the physical properties of the boranes and their derivatives (sixty pages) and a bibliography, classified by compound, of references to infrared, raman, nuclear magnetic resonance, ultraviolet, microwave, electron spin resonance and mass spectra, and to structural determinations and molecular orbital calculations (thirty-five pages). A brief section on carboranes is also included in each section and, in all, 1,400 references are cited.

A similar approach is adopted in subsequent chapters, the length of each reflecting the amount of work published: aluminium hydrides (sixty-two pages), other group III hydrides (nineteen pages), silanes (177 pages), germanes (eighty pages), stannanes (thirty-eight pages) and plumbanes (eight pages). There is also an appendix (keyed to the main chapters) reviewing the work which appeared in some 150 papers during the early part of 1970.

Throughout the book the diagrams are a particularly pleasing feature and they enhance the text considerably. The style of writing is impeccable and great attention has also been paid to the general

format, display of equations and clarity of print. Indeed the book is beautifully produced except for one ghastly mistake: in the review copy at least, pages 673–688 were missing and pages 641–656 were bound in twice. It is also unfortunate that the price will put the book out of the range of virtually all private individuals and most libraries. No doubt it will occur to many (however reprehensible the thought may be) that it could be Xeroxed for private study for less than one quarter of the published price always provided that a sufficiently affluent library could be located to borrow it from.

N. N. GREENWOOD

Glacial Ages

The Late Cenozoic Glacial Ages. Edited by Karl K. Turekian. Pp. xii+606. (Yale University: New Haven and London, August 1971.) \$20; £9.

THIS book is a collection of essays by leading authorities on diverse aspects of Cainozoic glacial ages, presented at an international colloquium held in 1969 to honour the retirement of R. F. Flint. The editor of the book, K. K. Turekian, points out that glacial ages are now known to have occurred before the classical glacial Pleistocene, and that it is therefore necessary to consider the phenomena associated with glaciation as properties of the Late Cainozoic. Much of the new evidence concerning environmental history in the Late Cainozoic comes from studies of ocean sediments and many of the twenty-one essays in the book concern this aspect of the subject. The essays thus supply a geophysical and marine geological background against which we may view the more classical aspects of the Quaternary ice ages.

There have been huge advances in our knowledge of Late Cainozoic environments, both marine and continental, in the past ten years; for example, the knowledge of climatic history provided by oxygen isotopes in marine faunas and in Arctic and Antarctic ice, and the knowledge of vegetational history provided principally by pollen analysis. The value of this book lies in the synthetic accounts written by those who have been responsible for much of the important research of the past two decades. It is not possible to make a detailed inventory of the contents. The essays concern the Late Cainozoic history of the oceans (including plate tectonics), and of Antarctica, the climatic records found in ice cores (a very important recent development), carbon-14 variations in the atmosphere, eustasy and isostasy, glaciation and vegetational history in North America, the floral record of the European Late Cainozoic, faunal history in Europe and Asia and hominoid evolution in East Africa.

The book thus provides an extremely valuable and timely synthesis of the present state of the many aspects and methods of study of environmental history in the Late Cainozoic. All the fields of research represented are advancing rapidly and workers in Quaternary research will be indebted to the organizers of this colloquium for providing them with a stimulating survey of recent achievements and prospects in the elucidation of Late Cainozoic Earth history. R. G. WEST

Gas/Metal Interface

Chemisorption and Reactions on Metallic Films. Edited by J. A. Anderson. Vol. 1: Pp. xii+555; £11; \$32. Vol. 2: Pp. xii+323; £7; \$21. (Academic: London and New York, August 1971.)

THESE two volumes comprise nearly 900 pages and cost £18 for a text that is well produced, except that almost every international convention regarding abbreviations, units and the printing of physical quantities in italic (or sloping) type, has been disregarded, and none of the authors has used SI units.

A book of this title fulfils a need and its appearance is timely. Its purpose is to describe with some degree of coherence and continuity the contributions to our understanding of the chemistry of the metal/gas interface in relation to the structure of metal films. The objective has only been partly achieved, because many of the authors have written about the topic of the chapter heading and have forgotten the principal title of the book. There is, in consequence, much valuable information about the formation and structure of films, and also about the chemisorption of gases on metal surfaces, but little correlation between these two groups. Each author has apparently been largely unaware of the contents of the other chapters, so that there is a fair measure of overlap and no overall coherence.

Scientists should first judge the relevance of the material about which they write and secondly express themselves concisely. There is little advantage to the reader in being presented with a series of review articles containing a large amount of descriptive detail both about the results and the workers who obtained them. Some judgment and critical assessment, even if biased, of the present status of the art are surely preferable.

In this respect, D. F. Klemperer's article is scholarly and critical; and he provides a well-organized account in admirably concise prose, yet the chapter is still extensively and well documented. The material is aptly chosen and is indeed directed to the use of metallic films as a primary consideration. J. V.

Sanders in his chapter on structure of evaporated metal films has also the interests of experimental surface chemistry in mind by concentrating on structure in relation to the deposition parameters in film preparation and he provides guide-lines for the control, at least in part, of porosity, grain size, the quality of epitaxial layers and so forth, while emphasizing that it is by no means clear what conditions of preparation will produce either facets of close-packed atoms, or randomly oriented surfaces with kink and ledge atoms; and their surface properties may be quite different.

In contrast, the two long chapters by J. W. Geuss on fundamental concepts in film formation and on the influence of adsorption on electrical and magnetic properties are expansive reviews, written in verbose style. Judged in isolation, these chapters contain much good material and have considerable merit; in terms of the chief theme of the book, one must question the relevance of much of its contents. It requires ingenuity to transpose information about migration of metal atoms over a field emission tip, or the thermal accommodation of such atoms on the cleavage plane of an ionic crystal, to the problem of chemisorption of a gas on metallic films. Many people have doubts about the assessment of conductivity results on films and of their theoretical interpretation in terms of adsorbate-adsorbent bonding, so that in terms of the price of the present volume, a much shorter chapter could have been more appropriate.

D. O. Hayward in his chapter on gas adsorption clearly has an important task to perform. Except for some short sections on heats of chemisorption and desorption spectra of gases from metallic films, he has largely confined attention to an undefined metallic plane or to specific planes of metal crystals. He panders to convention by a necessarily superficial account of band theory, and then reverts to localized band concepts and surface geometry as an explanation of different adsorption states. The recent literature is well reported but the reader is given little help in understanding the significance of the wealth of detail presented. With greater selectivity and better organization, and a more concise style, an even more valuable contribution would have resulted.

In the final chapter in the first volume on infrared spectra of surface species, J. H. Little provides an abbreviated version of his 1966 book. The contributions of Greenler, both theoretical and experiment, on the multiple reflectance technique, and the interferometric studies of Low, are, however, included. Nevertheless, the impression gained is that one should concentrate on oxide

surfaces in order to exploit more fully this technique.

J. Anderson (the editor) and B. G. Baker contribute the first two chapters in the second volume on adsorption, kinetics and surface structure and catalytic reaction on metal films. In the first chapter, a concise relevant account of structure, porosity, sintering and heterogeneity of films is followed by a good outline of equilibrium adsorption and rates of adsorption on a uniform surface as an introduction to an extension to heterogeneous surfaces. It has not been possible to treat reaction with films in an explicit manner, but at least the problem has been posed and recognized.

It is extremely difficult to write about catalytic reactions; the experimental data are varied and irreproducible, and to provide any general coherent theoretical account is not really possible. The reactions chosen are: exchange, hydrogenation, hydrogenolysis and skeletal isomerization, and oxidation and dehydrogenation. They are treated at a phenomenological level in an attempt to give a general understanding of the nature of catalytic reactions on metal surfaces and a guide to the vast literature on this subject; in this sense, the contribution is a valuable and successful one.

The final two chapters deal with the properties and reactions of alloy films by D. R. Rossington, and oxidation of evaporated films by I. M. Ritchie. The first of these is a very good article and is directed throughout to films. The preparation, characterization and structure of films, with particular reference to the composition of the surface, are reported competently before the sections on the surface properties and the catalytic activity in parahydrogen conversion, oxidation reaction and ethylene hydrogenation. The material has been well organized, selected with judgment, and presented with clarity.

Ritchie has written an interesting and critical chapter—it has a freshness, largely because of its selectivity and critical approach. Oxidation of metals precedes that of films; the limited information derived from purely kinetic relationships is emphasized and other approaches are examined. The concepts are then discussed in relation to films and the further restrictions on the interpretation of results by the film structure qualitatively examined in a workmanlike manner.

In conclusion, although the chief purpose of the book has only been partly attained, surface chemists interested in the gas/metal interface and in metallic films should use all their persuasive powers to ensure that a copy of this book is available in an accessible library. F. C. TOMPKINS

CORRESPONDENCE

Publication Speed

SIR,—Your recent editorial (*Nature*, **233**, 294; 1971) on multiple publication seems to me to put the responsibility of the journals for this practice at a lower value than the facts would merit. You merely suggest that the slowness of the whole process of publication has some effect on the willingness of scientists to "leak" to newspapers before publication. It is, however, quite clear that the frequent lack of efficiency in the processing of articles submitted to learned and technical journals could function as a strong incentive to submission of papers to several journals simultaneously. Old news is no news, in science as elsewhere, and scientists are concerned to have their material appear in print as quickly as possible. If journals appear to reject papers arbitrarily then there is, from the author's viewpoint, something to be gained from a course of action which avoids the possibility of being left six months or even a year behind the field with a perfectly good but homeless paper.

The experience of some members of this laboratory would certainly indicate the need for a certain amount of reform in the way journals are run. I myself am co-author of a paper submitted to a reputable journal in February 1970 which was at first rejected and then, having been refereed again, was accepted in a revised form. This took the remainder of the year although the actual rewriting took perhaps three weeks. This paper has still not appeared, after nearly two years. A second paper for the same journal has been refereed (this took seven months) and has just been rejected by an editorial fiat that the subject matter is not relevant to the journal's interest although the scientific merit is unquestioned. Why could this decision, if justified, not have been made by the editor when he received it? The nature of the subject matter was clear from the title and abstract. An article submitted for the features pages of the journal of an engineering institution was with the editor for three months, at the end of which time he had it set up in type, before he acknowledged receipt of the article. At this point he decided that it was more suitable for the proceedings and scientific papers section of the journal and sub-

mitted it to the papers committee of the institution. Another decision which would have been better made at the earliest opportunity.

If editors are willing to countenance in themselves such a lack of regard for the interests of contributors, then they must take the consequences, which may well include multiple publications. Authors should not be expected to sit helpless before this sort of treatment which, in many cases, decreases the value of their work. Editors should acknowledge receipt of papers, reply to authors' letters in less than the month which is common, should as a matter of course prompt referees into faster reading and should make their editorial as distinct from their scientific decisions at an early rather than a late date. They may then find themselves better served by contributors.

Yours faithfully,

I. D. GRIFFITHS

*The Electricity Council
Research Centre,
Capenhurst,
Chester*

Forecasting

SIR,—In your editorial "How Much is Enough?" (*Nature*, **234**, 115; 1971) you discuss the difficulty of forecasting population growth, and you ask whether the forecaster—in this case the Government Actuary—should "settle for more modest but more realistic goals". An interesting question, but not confined to the prediction of population.

In any organization concerned with products—schools, hospitals, food supplies, aircraft, weapons—of long gestation, there is always a wish to know the future so that policies can be tailored accurately to meet world conditions as they will exist ten or more years hence. And so there is pressure to forecast not only populations but also social and political attitudes, economic conditions, technological developments and so on.

When these questions are posed, they are answered: "forecasting" has achieved a respectability undreamt of by the seers of the Middle Ages. The forecasts provided become, too often, the single set of assumptions on which planning is based. If the forecast

should prove accurate, then the policy-makers are labelled "far sighted"; if not, they are, with hindsight, abused for having backed the wrong horse. But might it not be wiser to accept that forecasting is not an exact science. We have the evidence of grossly misleading population predictions; we know that political attitudes can change markedly within a few months; social attitudes appear essentially unpredictable in the longer term; technological forecasts merely reflect an obvious truth that the more money and effort is poured into any project the faster it will move. Against this sort of background, might it not be that the sensible approach is to seek to build a system reasonably matched to a wide range of possible futures rather than closely matched to a single predicted future?

Yours faithfully,

I. J. SHAW

*"Woodilee",
Mellersh Hill Road,
Wonersh Park,
Guildford, Surrey*

Protecting Potatoes

SIR,—Under the headline "A Sticky End" (*Nature*, **233**, 93; 1971) your correspondent gave recognition to an interesting piece of work by Dr R. W. Gibson on the part played by glandular hairs in providing resistance to aphids in three species of potatoes (*Ann. Appl. Biol.*, **68**, 113; 1971). Gibson showed that glandular hairs on the potato species *Solanum berthaultii*, *S. tarijense*, and *S. polyadenium* discharged a gummy exudate which eventually immobilized the aphid and led to its death through starvation. As noted by Gibson this type of mechanism has potential value in the control of aphid population build-up. This effect may be further enhanced if combined with other types of resistance to aphids, such as the resistance to feeding demonstrated in several potato species, including *S. polyadenium*, by J. B. Adams at this research station. Control of aphid populations in such ways as these has the additional effect that it reduces the rate of spread of certain aphid-borne viruses.

The key to the utilization of these

traits lies in the practicality of incorporating them into the parental lines used in potato breeding programmes. Gibson recognized this, and noted that *S. tarijense* may be crossed with the cultivated potato. Your correspondent, however, gives the impression that the problems in utilizing these species are completely unknown. This is far from the case.

S. berthaultii and *S. tarijense* are diploid species and both can be crossed easily with the cultivated potato, the tetraploid *S. tuberosum*. The progeny from such crosses are sterile triploids which would still carry many undesirable traits from the wild species. However, both these species can also be crossed with haploids (dihaploids) of *S. tuberosum*, and with haploid derivatives, to give progeny which are diploid and, when the wild species is used as the seed parent, are also generally fertile. Undesirable traits may be eliminated by further crossing and selection. *S. polyadenium*, on the other

hand, can at best only be crossed with *S. tuberosum* with very great difficulty.

It is clear that of the species studied by Gibson two, *S. berthaultii* and *S. tarijense*, can be used in a breeding programme fairly readily. Working at the diploid level, as I have suggested, has numerous advantages, and there are several methods of combining diploid parental lines and tetraploid cultivars at the final stage before variety selection.

Yours faithfully,

T. RICHARD TARN

Canada Department of Agriculture,
Research Station,
Fredericton, New Brunswick

Unambiguous Billion

SIR,—For a long time we have had to live with the annoying fact that Americans and Europeans cannot use the word billion without a risk of confusion. Perhaps it would be possible to persuade people on both sides of the Atlantic to

add just two extra letters to indicate how big the billion is meant to be. To be specific, I suggest that 1 ambillion = 10^9 and 1 eubillion = 10^{12} . Thus ambillion becomes the name of the American billion—a cause of ambiguity.

Yours faithfully,

J. HILDEN

Department of Statistics,
University Institute of Medical Genetics,
Copenhagen

Retino-rectal Connexions

SIR,—Dr Robertson (*Nature*, 233, 435; 1971) refers to an annoying visual condition which he calls tunnel vision. Surely he means hindsight?

Yours faithfully,

F. H. ALLEN

N. W. ISAACS

University Chemical Laboratory,
Lensfield Road,
Cambridge CB2 1EW

Obituary

Professor Arne Tiselius

PROFESSOR ARNE TISELIUS, who won the Nobel Prize for chemistry in 1948, died in Stockholm on October 29, aged sixty-nine.

Born in Stockholm in 1902, Tiselius moved early to Gothenburg and thence, after matriculation, to take up academic studies in Uppsala, the city which he was rarely to leave. Tiselius's interest in chemistry was first awakened at school, and his ability was noticed by The Svedberg, who quickly made him his valued and trusted research assistant. The master soon gave his protégé the freedom to plan and carry out his research. Tiselius chose to investigate electrophoresis and studied in particular the so-called boundary anomalies which occur in connexion with the electrophoretic migration of proteins. In his doctoral dissertation in 1930, Tiselius presented significant discoveries on the heterogeneity of serum proteins. After an important year of research at Princeton, he continued his development of moving boundary electrophoresis and designed the apparatus which made his name internationally known, the chief improvement being the elimination of convection. Tiselius showed by means of this apparatus that the electrophoresis of serum gave five distinctly migrating boundaries. These are albumin, and α , β and γ globulin as Tiselius designated them, and also a boundary dependent on the protein concentration. This work brought the world's leading immunochemists to Uppsala and the international

contacts in many fields of physical chemistry and biochemistry were intensified. In 1938 Tiselius became the first to hold a newly created research chair in biochemistry at Uppsala.

Tiselius took an active part in the development of electrophoresis and especially preparative zone electrophoresis, but he extended his interest to chromatography which he realized was to provide biochemists with the necessary methods for further investigating the chemistry of proteins. He introduced a standard nomenclature for chromatography and contributed especially to the development of general principles for analytical and preparative chromatography.

For example, displacement chromatography and gradient chromatography originate from Tiselius's pioneer work. Gas chromatography can also be traced from the Uppsala school. These methods have extended far beyond the field of protein chemistry. Tiselius's last work as an active researcher was to investigate suitable conditions for the chromatography of proteins. His contribution was the introduction of calcium phosphate as an adsorbent, which method is still being used. When ion-exchangers and molecular-sieving gels were introduced he retired from experimental work but followed developments with never ending interest and gave generously of his knowledge to others.

After receiving the Nobel Prize in 1948 Arne Tiselius increasingly began to devote himself to research policy. He was President of the International Union of Chemistry IUPAC from 1951–1955.

Swedish science is greatly indebted to Arne Tiselius. He was, for example, one of the initiators for the founding of the Swedish Natural Science Research Council.

He became the presiding chairman of the Royal Academy of Science in 1956 and was very active in the Nobel Foundation, and held, among other posts, the chair between 1960–64. He took a keen interest in the Foundation's symposium committee and took the initiative for several of the international symposia. He was also a member of the Wallenberg Foundation.

Tiselius's contributions to the international coordination of research in chemistry have been of utmost importance and the appreciation resulted in eleven honorary degrees. He belonged to a great number of academies and learned bodies and was on the editorial committees of a number of scientific journals. His capacity for work was almost unbelievable and he was always in great demand.

Tiselius was deeply and personally involved in the problems arising from the effects of scientific research on society and man, and he expressed his anxieties for the negative effects in the Pugwash movement.

Arne Tiselius was not only a brilliant scientist, but also an unusual personality. He possessed a rare ability for listening to others' opinions, drawing conclusions, seeing the essentials, summarizing and then presenting the judgment and advice of a good friend and wise leader. He will be sorely missed.

Announcements

International Meetings

December 28–31, **Association for Science Education Meeting**, Stirling (Mr J. Keri Davies, Education Department, University of Stirling, Scotland).

January 4, 1972, **Plant Constituents of Pharmacological Interest**, London (Mr R. E. M. Marshall, Pharmaceutical Society, 17 Bloomsbury Square, London WC1).

January 4–7, 1972, **Society for Experimental Biology Conference**, London (Mr T. M. Preston, Department of Zoology, University College, Gower Street, London WC1).

January 5–7, 1972, **Increasing the Biological Contribution to the Control of Pests and Diseases**, Oxford (Society of Chemical Industry, 14 Belgrave Square, London SW1).

January 6–7, 1972, **Biology of the Cell Membrane**, Amsterdam (Dr J. James, Histological Laboratory, Jan Swammerdam Institute, 1st Constantijn Huygensstraat 20, Amsterdam, Holland).

January 7, 1972, **Sampling of Mineralogical and Geological Materials**, London (The Secretary, The Institute of Mining and Metallurgy, 44 Portland Place, London W1N 4BR).

January 10–12, 1972, **Surface Physics of Semiconductors**, Southampton (Dr D. R. Lamb, Department of Electronics, University of Southampton, Southampton SO9 5NH).

January 11, 1972, **Unconventional Nitrogenous Sources for Feeds and Foods**, London (Mr N. R. Jones, BFMIRA, Randalls Road, Leatherhead, Surrey).

January 18, 1972, **The Prevention of Air Pollution from Incineration**, Manchester (The Filtration Society, 1 Katharine Street, Croydon CR9 1LB).

January 25, 1972, **Lipoprotein Phenotyping**, London (Dr B. Lewis, Department of Chemical Pathology, Royal Postgraduate Medical School, Ducane Road, London W12 0HS).

February 21–25, 1972, **Photo Interpretation for Industry and the Environment**, London (N. Lindsey, The City University, St John Street, London EC1V 4PB).

February 23, 1972, **Anaesthetic and Neuro-muscular Blocking Drugs**, London (Dr A. B. Simmonds, Chelsea College, Manresa Road, London SW3).

Reports and Publications

not included in the Monthly Books Supplement

Great Britain and Ireland

Royal Observatory Bulletins. No. 162: Optical Positions of Radio Sources. By C. A. Murray, R. H. Tucker and E. D. Clements. Pp. 215–238. 50p net. No. 164: The Isaac Newton Telescope Cassegrain Spectrograph. By G. A. Harding and M. P. Candy. Pp. 251–256. 20p net. No. 166: The Statistics of the Nearby Stars. By Sir Richard Woolley, Susan B. Pocock, Elizabeth A. Epps and Rosalind Flinn. Pp. 275–299. 40p net. (Herstmonceux: Royal Greenwich Observatory, 1971.) [238]

Forestry Commission. Library Catalogue of Books. Pp. 176. Horticultural Uses for Bark. Pp. 8. Research and Development Paper No. 81: Forest Management for Conservation, Landscaping, Access and Sport. Pp. 30. (London: Forestry Commission, 1971.) [248]

Philosophical Transactions of the Royal Society of London. B: Biological Sciences. Vol. 262, No. 842 (20 August 1971): A Discussion on Active Transport of Salts and Water in Living Tissues. Organized by R. D. Keynes, FRS. Pp. 83–342+plates 23–35. (London: The Royal Society, 1971.) £7.80; \$20.30. [248]

Shipbuilding and Shiprepairing. Pp. 10. (London: Commission on Industrial Relations, 1971.) [268]

Trada 70—Report of the Director of the Timber Research and Development Association. Pp. 12. (London: Timber Research and Development Association, 1971.) [268]

Political and Economic Planning. Broadsheet 530: Work Camps and Volunteers—The PEP Study of International Work Camps in Britain and British Work-Camp Volunteers. By Michael Thomas. Pp. iii+93. (London: PEP, 1971.) £1. [278]

Science Research Council. Royal Observatory, Edinburgh. Publications—Vol. 7, No. 5: Photographic V and R Magnitudes of T Tauri Stars and Related Objects in Orion. By M. T. Brück. Pp. 63–72. (Edinburgh: The Royal Observatory, 1971.) [278]

Philosophical Transactions of the Royal Society of London. B: Biological Sciences. Vol. 262, No. 843: Ontogenesis of Corneal Surface Ultrastructure in Nocturnal Lepidoptera. By G. Gemme. Pp. 343–363+plates 36–53. £2; \$5.20. Vol. 262, No. 844: Synaptic Organization of Cone Cells in the Turtle Retina. By A. Lasansky. Pp. 365–381+plates 1–8. £1.70; \$4.40. (London: The Royal Society, 1971.) [278]

The Zoological Record, 1969, Vol. 106, Section 8: Bryozoa (Polyzoa) and Entoprocta. Compiled by the Staff of the Zoological Society of London. Pp. iv+16. (London: The Zoological Society of London, 1971.) £3.50. [318]

Environmental Studies: The Construction of an 'A' Level Syllabus. Compiled by S. McB. Carson. Pp. 158. (London: National Foundation for Educational Research in England and Wales, 1971.) £1 (by post £1.10). [318]

British Medical Bulletin, Vol. 27, No. 3 (September 1971): Symposium on "Cognitive Psychology". Pp. 191–290. (London: The British Council, 1971.) £2. [318]

The Hannah Dairy Research Institute. Report for the Three Years ended 31st March, 1971. Pp. 78. (Ayr: The Hannah Dairy Research Institute, 1971.) [319]

Calendar of the Countryside for 1972. (London: Christian Action Publications Limited, 1971.) 75p (postage 5p). [319]

The Scottish Horticultural Research Institute. 17th Annual Report for the year 1970. Pp. 69. (Invergowrie, Dundee: The Scottish Horticultural Research Institute, 1971.) [329]

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